FINAL REPORT

Community and Ecosystem-level Effects of Growing v. Dormant Season Burning in the Southern Appalachians

JFSP PROJECT ID: 16-1-06-12

June 2021

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List of Abbreviations/Acronyms	
C: Control (unburned)	KBDI: Keetch-Byram Drought Index
DEM: Digital Elevation Model	NMDS: Nonmetric Multidimensional Scaling
dNBR: Difference Normalized Burn Ratio	RAWS: Remote Automatic Weather Station
DS: Dormant season burn	RH: Relative humidity
GS: Growing season burn	RMSE: Root mean squared error
HLI: Heat Load Index	SE: Standard error
IV: Importance value	TPI: Topographic Position Index

Keywords

Diversity, duff, fire weather, fuel moisture, litter, mountain laurel, red maple, topography, vegetation, woody fuels

Acknowledgments

The authors would like to thank the USDA Forest Service, Francis Marion and Sumter National Forests, Andrew Pickens Ranger District and the Chattahoochee-Oconee National Forests, Chattooga River Ranger District for permission to collect field data and for conducting the prescribed fire treatments. Input and feedback were given by S. Norman and R. Klein, who improved earlier versions of the manuscript by offering new considerations and providing context. Thank you to T. Waldrop who helped to develop the research methodology and to J. O'Brien and B. Buchanan who provided helpful feedback along the way. The authors appreciate the efforts of E. Oakman, T. Trickett and G. Chapman in establishing plots, developing protocols, and collecting field data in the first year of this project. The authors would further like to acknowledge the many undergraduate and graduate students who assisted with data collection.

Abstract

Despite the widespread use of prescribed fire throughout much of the southeastern United States, temporal considerations of fire behavior and its effects often remain unclear. Opportunities to burn within prescriptive meteorological windows vary seasonally and along biogeographical gradients, particularly in mountainous terrain where topography can alter fire behavior. Managers often seek to expand the number of burn days available to accomplish their management objectives, such as hazardous fuel reduction, control of less desired vegetation, and wildlife habitat establishment and maintenance. For this study, we compared prescribed burns conducted in the dormant and early growing seasons in the southern Appalachian Mountains to evaluate how burn outcomes may be affected by environmental factors related to season of burn. The early growing season was defined as the narrow phenological window between bud break and full leaf-out. Proportion of plot area burned, surface fuel consumption, and time-integrated thermocouple heating were quantified and evaluated to determine potential relationships with fuel moisture and topographic and meteorological variables. Additionally, treatment effects on plant groups were distinguished by growth habit, tree group, life history, and management species of interest.

Our results suggested that both time-integrated thermocouple heating and its variability were greater in early growing season burns than in dormant season burns. These differences were noted even though fuel consumption did not vary by season of burn. The variability of litter consumption and woody fuelbed height reduction were greater in dormant season burns than in early growing season burns. Warmer air temperatures and lower fuel moisture, interacting with topography, likely contributed to these seasonal differences and resulted in more burn coverage in early growing season burns than in dormant season burns. Season of burn had few significant effects on understory plant cover, density, richness, or diversity. In the midstory, early growing season burns were more effective than dormant season burns at reducing shrub stem density, with the greatest differences observed in the smallest size classes. Early growing season burns reduced midstory red maple stem density to a greater extent than dormant season burns, though this pattern was not observed for other mesophytic hardwood species.

Dormant season and early growing season burns in southern Appalachian forests consumed similar amounts of fuel where fire spread. Notwithstanding, warmer conditions in early growing season burns are likely to result in fire spread to parts of the landscape left unburnt

in dormant season burns. By nearly all metrics, early growing season burns had similar effects on understory vegetation as dormant season burns – but had greater impacts on the midstory. Overall we conclude that early growing season burns may offer a viable option for furthering the pace and scale of prescribed fire to achieve management objectives.

Objectives

For this study, we assessed how of season of burn influences fire behavior, fuel consumption, species cover, density and diversity. Treatments included replicated 1st entry burn (dormant season, early growing season) and unburned control treatments across landscape-scale management units. Data were collected to address the following questions:

- 1. How do meteorological conditions influencing surface fuel moisture and proportion of plot area burned vary by season of burn?
- 2. How do time-integrated thermocouple heating, surface fuel consumption, and the relationship between these variables differ by season of burn?
- 3. How are slope position and solar heat load related to fire behavior in dormant and early growing season burns?
- 4. How does season of burn affect absolute plant cover and/or density in understory, midstory, and/or overstory vegetation strata?
 - a. By growth habit (forb, graminoid, shrub, tree, vine)?
 - b. By tree group (hickory, mesophytic hardwood, red oak, white oak, white pine, yellow pine, other)?
 - c. By life history of woody plants (germinant, established, sprout)?
 - d. By management species of interest (red maple, mountain laurel)?
- 5. How does season of burn affect species richness and diversity $(\alpha, \beta, \text{ and } \gamma)$ in understory and midstory strata?
- 6. How does season of burn affect canopy cover?
- 7. Which environmental factors best explain relative shifts in community composition as related to season of burn in understory and midstory strata?

For Question #1, we hypothesized that diurnal solar radiation and average ambient temperatures would be higher in the early growing season, resulting in lower surface fuel moisture and a greater proportion of treatment area burned than in the dormant season.

For Question #2, we hypothesized that the degree and variability of time-integrated heating would be greater in early growing season burns than in dormant season burns. We also hypothesized that the degree and variability of litter and fine woody fuel consumption would be greater in early growing season burns, driven by variations in fuel moisture. Furthermore, we expected that litter and duff consumption would rise at a greater rate with increasing time-integrated heating (have a steeper slope between these variables) in dormant season burns than in early growing season burns.

For Question #3, we hypothesized that bole char height would rise at a greater rate with both increasing slope position and increasing solar heat load (have steeper slopes between these pairs of variables) in dormant season burns than in early growing season burns. Furthermore, we expected that bole char height would be more strongly correlated with both slope position and solar heat load in dormant season burns than in early growing season burns.

For Question #4, we hypothesized that forb and graminoid cover and density would increase the greatest following early growing season burns in comparison to dormant season

burns. We also hypothesized that effects on woody vegetation would be greatest for red maple and other mesophytic hardwoods, with a greater decrease in stem density in the early growing season. We further expected increases in germinant and sprout density of woody stems relative to those established of the same vegetation following a single burn treatment. Herbaceous species, often dominant in earlier stages of succession, may respond more positively following growing season burns due to (a) more favorable photoperiod and temperature for regrowth and flowering (Platt, Evans, and Davis 1988; Streng, Glitzenstein, and Platt 1993) and (b) decreased abundance of competing woody species post-fire than in dormant season burns (Knapp, Estes, and Skinner 2009). Slower growing woody species may be less sensitive to seasonal differences in growing conditions prior to full leaf-out unless burn treatments can significantly increase canopy openness (Keyser, Greenberg, and McNab 2019).

We hypothesized that there will be greater decreases in midstory stem density (including red maple and mountain laurel) with early growing season burns than dormant season burns. Therefore, drier fuels and greater temperatures observed in the early growing season (Vaughan et al. in review) suggest that higher intensity fires (more likely later in the year before full leaf-out) will result in greater midstory mortality, particularly of stems of the smallest size classes. We further expected that early growing season burns will result in greater decreases in midstory cover and mountain laurel height than dormant season burns.

For Question #5, we hypothesized that species richness and diversity would be significantly greater following early growing season burns than dormant season burns. We expected this difference to be primarily driven by both (a) greater increases in the relative abundance of forbs and graminoids and (b) greater decreases in the relative abundance (reduction in dominance) of certain woody species, including mesophytic hardwood trees, in the early growing season than in the dormant season.

For Question #6, we hypothesized that change in canopy cover would not significantly differ by season of burn. Differences between burn treatments in the abundance and diversity of understory vegetation would, therefore, be expected to be explained by factors other than decreases in canopy cover that may occur.

For Question #7, we expected that environmental gradients related to fire behavior will explain seasonal variability in community response between burn treatments. We hypothesized that topographic measures of slope position and heat load will explain a greater degree of variability in plant community composition in the dormant season than in the early growing season.

Our questions and hypotheses are related to the JFSP-identified task statement by examining the effects of prescribed fires in different seasons on short-term management objectives related to fuels and vegetation in the region of the Consortium of Appalachian Fire Managers and Scientists.

Background

Fire is firmly embedded in the natural history and human experience of the American Southeast. Evidence suggests that fire has been prevalent in the Southeast for millennia, from the written accounts of explorers who described pervasive smoke and open woodlands (Fowler and Konopik 2007), to reconstructions of past fire occurrence using physical measurements synthesized by researchers (Delcourt and Delcourt 1998, Lafon et al. 2017). Humans before and

after Euro-American settlement in the 1700s and 1800s used fire to cultivate habitat for their livelihood (Owsley 1949, Stewart 2002, Abrams and Nowacki 2008), fostering a culture of burning that may inform our present treatment of fire. Recognizing that decades of fire suppression in the 1900s often led to hazardous fuel accumulation and forest "mesophication" (Nowacki and Abrams 2008), policymakers and land managers have increasingly endorsed and implemented prescribed fire in recent decades to reduce wildfire risk and promote ecosystem health and resiliency (Pyne 1982, Rothman 2007, Waldrop and Goodrick 2012). Today, more area is treated with prescribed fire on an annual basis in the Southeast than in any other region of North America (Wade et al. 2000, Kobziar et al. 2015, Melvin 2018).

Wildland fire is thought to have occurred more often in different seasons prior to fire suppression than it does today, particularly in the Southeast's most fire-prone environments (Komarek 1965, 1974; Lafon 2010). Habitats favorable to forage and harvest could have been maintained by humans burning in a variety of seasons (Eldredge 1911, Jurgelski 2008). Historically, lightning ignitions may have occurred in drier fuels under more open canopies, a potential source of fire following spring and summer thunderstorms (Barden and Woods 1974, Cohen et al. 2007). Lightning-ignited fires in the southern Appalachians were unlikely to have been common, however, and wet weather would typically constrain their spread (Lafon et al. 2017). Wildland fire extent in largely deciduous forests of the southern Appalachians today is inversely related to vegetation greenness (Haines et al. 1975, Norman et al. 2019), with most area burned either in late winter (dormant season) and spring before complete leaf expansion (early growing season) or in the fall following leaf abscission (Schroeder and Buck 1970). Fire seasonality is further confounded in mountainous topography with less predictable fire behavior due to more heterogeneous temperature and moisture conditions across the landscape (Stambaugh and Guyette 2008, Lesser and Fridley 2016).

The use of prescribed fire has expanded substantially in the southern Appalachians in recent decades amid widespread efforts to reduce hazardous fuel loads, restore woodland and savannah communities, and increase native oak (Quercus L.) and yellow pine (Pinus L.) regeneration (Van Lear and Waldrop 1989, Waldrop and Brose 1999, Brose et al. 2001). Using fire for these objectives has largely occurred in the dormant season before substantial spring green-up, mirroring prescriptive patterns of fire use in the Southeast more broadly (Van Lear and Waldrop 1989, Wade and Lunsford 1989). Burning in the dormant season as opposed to the growing season may decrease the risk of fire escape, particularly in mid-late winter with lower ambient temperatures and more predictable wind patterns (Mobley and Balmer 1981, Wade and Lunsford 1989, Robbins and Myers 1992). Spring burning has also been less favored due to potential detrimental effects on wildlife species that may be more vulnerable to fire during that stage of their life history (Landers 1981, Cox and Widener 2008). In light of the prevalence of dormant season burning, potential growing season fire behavior and effects are not well understood (Knapp et al. 2009, Reilly et al. 2012). However, there is likely a window in the early growing season when dry forest floor conditions permit the combustion of fuels and spread of fire – perhaps to a greater extent than would occur under typical dormant season burning conditions. For managers in the southern Appalachians who want to expand their prescribed fire programs, growing season burning could offer an alternative to dormant season burning, allowing for increased opportunities to burn. Evidence of historical fire regimes suggests fire occurrence outside of the dormant season (Lafon et al. 2017, Stambaugh et al. 2018). It remains to be seen, however, how growing season burns compare to dormant season burns for accomplishing management objectives of reducing fuel loads and restoring habitats.

Season of burn may influence patterns of forest succession through variable fire behavior and by altering the resource environment of plants in different phenological periods. Underlying physiological and morphological traits influence the vulnerability of plants to fire, with some species being more susceptible to damage or mortality than others (Bär et al. 2019; Grime 1977; Clarke et al. 2013). Species that can rapidly regenerate following fire may displace more fire-sensitive competitors, particularly in seasons corresponding to a favorable environment for new growth (Platt et al. 1988; Hiers et al. 2000). Alternatively, plants may need to replace a greater amount of lost energy during a growing season fire, siphoning vital resources that unburned plants would not have to expend before entering dormancy in the fall (Regier et al. 2010). Both immediate (first order) and delayed (second order) injuries may be caused by variable exposure of plant structures to heating and ultimately cause mortality (Michaletz and Johnson 2007; 2008).

Fire in different seasons may further alter patterns of succession by stimulating or suppressing the development of latent vegetation. Reductions in surface fuels by fire can provide new opportunities for the establishment of plants that were previously suppressed (Phillips and Waldrop 2008; Hutchinson 2006). Dormant seeds in the soil and those to be dispersed by established plants post-fire may be more likely to germinate and establish as a result of increased access to light and warmer temperatures (Baskin and Baskin 1988; Silvertown 1980). Alternatively, seeds recently dispersed may be consumed by fire on the soil surface, thereby reducing the pool of seeds of a given species that could establish in that season. (Dayamba et al. 2010). For example, red maple (*Acer rubrum* L.) seeds are typically dispersed by April in the southern Appalachians, eastern white pine (*Pinus strobus* L.) seeds disperse in the late summer and fall (September-October) (Wendel and Smith 1990; Krugman and Jenkinson 1974), and yellow-poplar (*Liriodendron tulipifera* L.) seeds are dispersed throughout the fall and winter (October-March) (Beck 1990). Consideration of how prescribed fire influences seedling recruitment may suggest which seasons of burn would be most effective for shifting plant community composition in desirable directions.

Improved knowledge of how and why fire behavior and effects vary seasonally may improve southern Appalachian forest management. Variability in meteorological and topographic factors influencing fire behavior may suggest the extent to which prescribed fire would be effective in achieving fuel load reduction, a first-order fire effect (Reinhardt and Keane 2009, Kreye et al. 2020). Solar radiation drives the magnitude and extent of surface fuel drying and thereby influences fire behavior relative to latitude, slope, and aspect (Byram and Jemison 1943). Slope position further influences the level and duration of heating from fire along moisture gradients from sheltered coves to prominent peaks across a mountainous landscape (Reilly et al. 2012, Dickinson et al. 2016). The effects of topography on fire behavior and resulting fuel consumption may also be reinforced or overridden by changing weather patterns over phenological transitions (Norman et al. 2017). Upon longer and warmer spring days, aboveground perennial emergence and heightened plant transpiration may lead to greater variability in the distribution of live fuel moisture (Jolly and Johnson 2018). In autumn, surface winds under an open canopy following leaf fall may compound moisture loss on upper slopes and ridges, creating a fuel bed more conducive to high rates of fire spread (Dickinson et al. 2016, Kreye et al. 2020). Fuel moisture alters flammability and may suggest fine-scale differences in fire effects (Sparks et al. 2002, Slocum et al. 2003, Kreye et al. 2018).

Methods

Study Area

This study was conducted along the southern Blue Ridge Escarpment of the Appalachian Mountains in the southeastern United States. Treatment replicates were located in both the Chattooga River (CR) Ranger District of the Chattahoochee National Forest in Rabun and Stephens Counties, Georgia, as well as the Andrew Pickens (AP) Ranger District of the Sumter National Forest, in Oconee County, South Carolina (Figure 1). Unit elevations ranged from 222 m to 1430 m, encompassing a variety of landforms from lower slopes in sheltered coves to exposed ridges and upper slopes of high peaks. Mean monthly temperatures ranged from 4 °C in January to 24 °C in July, with mean annual precipitation of 159 cm distributed relatively evenly throughout the year (NCEI 2020). Ultisols, Inceptisols, and Entisols were common soil orders found within the study area, mostly underlain by metamorphic bedrock (e.g. granitic gneiss and schist) (Griffith et al. 2001, 2002).

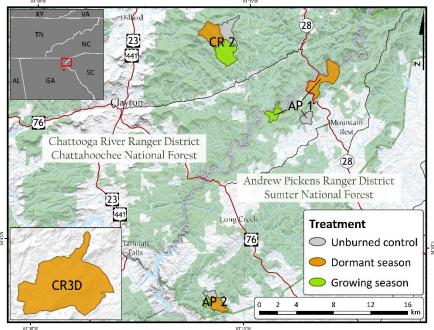


Figure 1. Map depicting the replicates comprised of treatment units with plots established in this study. "AP" refers to replicates in the Andrew Pickens Ranger District whereas "CR" refers to replicates in the Chattooga River Ranger District. Vegetation data were not collected in CR3D. See Table 2 for further information on treatment units.

Pre-treatment fuel characteristics were quantified prior to treatment (Table 1; see Fuel loads and depths section below). Forest cover consisted primarily of oaks (*Quercus* L.), hickories (*Carya* L.), and pines (*Pinus* L.) across the following ecozones (Simon et al. 2005, Simon 2015): Dry-Mesic Oak-Hickory Forest, Shortleaf Pine-Oak Forest and Woodland, Mixed Oak / Rhododendron Forest, and Montane Oak-Hickory Forest. Substantial midstory encroachment was present from mesophytic hardwoods [e.g. red maple (*Acer rubrum* L.)], mountain laurel (*Kalmia latifolia* L.), and great rhododendron (*Rhododendron maximum* L.).

Table 1. Summary of pre-treatment fuel characteristics between designated treatments across all study plots.

Woody fuel characteristic (Brown 1974)	Designated treatment	Mean (± SE)	Overall mean (± SE)
	С	6,707.2 (± 330.2)	
Litter load [kg ha ⁻¹]	DS	6,876.7 (± 292.2)	6,684.4 (± 179.7)
[Mg Mu]	GS	6,453.1 (± 315.4)	
	С	13.0 (± 1.2)	
Woody fuelbed height [cm]	DS	14.7 (± 1.3)	$14.1~(\pm~0.7)$
[em]	GS	14.6 (± 1.1)	
	С	551.1 (± 26.8)	
1-hr woody load [kg ha ⁻¹]	DS	619.1 (± 32.1)	604.4 (± 19.8)
[1.5]	GS	642.0 (± 41.8)	
	С	1,662.0 (± 127.2)	
10-hr woody load [kg ha ⁻¹]	DS	2,191.3 (± 174.2)	1,881.7 (± 90.9)
[Kg nu]	GS	1,765.9 (± 157.7)	
	С	3,493.8 (± 390.0)	
100-hr woody load [kg ha ⁻¹]	DS	6,355.4 (± 1,014.9)	4,941.0 (± 421.0)
[Kg Mu]	GS	4,856.0 (± 519.4)	
	С	6,356.4 (± 1,189.2)	
1,000-hr woody load [kg ha ⁻¹]	DS	5,480.3 (± 887.6)	5,457.6 (± 540.6)
[5]	GS	4,534.0 (± 665.0)	

Study Design

The study was established as a randomized complete block design, with treatments of dormant season burn (d), growing season burn (g), and an unburned control (c) replicated (blocked) three times. A fourth, standalone, dormant season burn in a planned, additional replicate was also included to equal a total of 10 treatment units. Treatment units ranged in area from 43 ha to 567 ha, with a mean area of 293 ha (Table 2).

Table 2. Listing of treatment units used in this study by replicate and corresponding treatment, with area, date of burn (if applicable), and elevation range. Firing methods included both hand ignition and remote aerial ignition, with a spot fire technique used for hand ignitions when possible to simulate aerial ignition.

Replicate Treatment	Unit	Area	Date of	Elevation	
Keplicate	Treatment	Omt	(ha)	burn	range (m)

	Unburned control (C)	AP1C	133.8	n/a	498 - 625
AP 1	Dormant season burn (DS)	AP1D	538.1	01/31/18	480 - 772
	Growing season burn (GS)	AP1G	160.5	04/18/18	454 - 560
	Unburned control (C)	AP2C	80.8	n/a	360 - 470
AP 2	Dormant season burn (DS)	AP2D	205.3	03/18/19	275 - 468
	Growing season burn (GS)	AP2G	43.3	04/21/18	312 - 462
	Unburned control (C)	CR2C	323.2	n/a	704 - 1,157
CR 2	Dormant season burn (DS)	CR2D	441.5	04/05/18	724 - 1,430
	Growing season burn (GS)	CR2G	435.3	04/24/19	622 - 963
CR 3	Dormant season burn (DS)	CR3D	566.5	03/03/18	222 - 386

Twenty plots were stratified across a variety of slope, aspect, and landscape positions within each treatment unit (except for 5 plots in the standalone unit). This yielded 180 plots with usable data that were included in analyses, with 5 plots in burn treatment units lost due to construction of control lines which contained different areas than had been anticipated. Each plot was 30 m x 30 m (900 m²), subdivided into nine 10 m x 10 m (100 m²) subplots delineated by 16 grid point intersections and oriented with outer boundaries running magnetic north (0°) and east (90°) from its point of origin (Figure 2). Surface fuel transects (15.24 m in length) were superimposed on each plot, separated by 20° magnetic azimuth emanating from the plot origin.

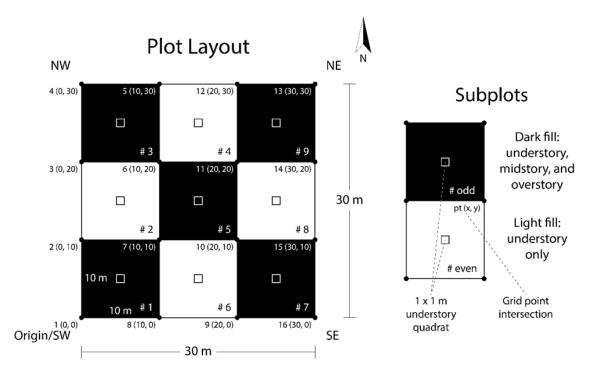


Figure 2. Representative diagram indicating the layout, orientation, and dimensions of each plot with interior grid point intersections, subplots, and understory quadrats. The (x, y) Cartesian coordinate pairs for each grid point represent the

longitudinal (x) and latitudinal (y) distance from origin. Brown's fuel transects (not shown) originated from the origin of each plot.

Prescribed burns were implemented by U.S. Forest Service fire practitioners as a part of official burn plans and coordinated with Clemson University for purposes of this study. Dormant season burns were defined as those occurring after autumn leaf-fall and before spring green-up (typically before last frost), whereas growing season burns were considered as those occurring in the early spring green-up period (typically after last frost) before complete overstory leaf-out. At the elevations of the study area, green-up typically begins in early April, with full leaf-out occurring by May. Burn treatments occurred between January 31 – April 5 (dormant season) and April 18 – 24 (growing season) in 2018 and 2019 (Table 2). Firing methods included hand ignition using drip torches as well as remote aerial ignition using delayed aerial ignition devices launched from a helicopter on some burns. A spot fire technique was used for hand ignitions when possible in order to simulate aerial ignitions.

Field Sampling and Data Preparation

Fuels were measured before and after each burn to determine changes in surface fuel load across all plots. Complementary measurements of litter and duff consumption were taken at a greater sampling density in a subset of plots (see Fuel loads and depths section below). Fuel moisture was sampled the morning of burns and levels of heating were recorded throughout each burn day in situ in the same subset of "fire behavior plots." Measurements of bole char height were taken in all plots following each burn. Visual evidence of the presence or absence of fire (y/n) was noted at grid point intersections, with a 50% threshold of grid points indicating the presence of fire used to qualify burn treatments for plot-level variables. The proportion of plot area burned was calculated by dividing the number of grid points with evidence of charred material by the total number of grid point intersections within a plot.

Fuel measurements of woody fuelbed height and fine woody debris counts (1-hr, 10-hr, and 100-hr) were taken in the growing season pre- and post-burn using a modified version of Brown's Planar Intercept Method (Brown 1974, Stottlemyer 2004, Coates et al. 2019). This method was utilized in all plots within the treatment units (3 transects per plot; n = 60 measurement units per treatment unit), which included measurements taken at designated intervals along transects emanating from the plot origin (3.66 m, 7.62 m, and 12.19 m). Slope values were derived from a digital elevation model along lines representing the length and orientation of each transect in a geographic information system (Esri 2019). Measurements of litter and duff consumption were taken at grid point intersections within a subset of 5 fire behavior plots per burn treatment (16 litter and 16 duff nails per plot; n = 80 measurement units for each fuel class per treatment unit) using depth reduction measurements on 30 cm nails. Nails for this purpose were driven into the ground prior to ignition so that the heads were at the same pre-burn height as the fuel class being measured. Post-burn fuel height was marked on the nail within 24 hours after burn completion to determine changes in litter and duff depth. All fuel depth and height measurements were recorded to the nearest 0.64 cm.

Raw fuel measurements were used to estimate fuel weight per area (load) for each fuel class, calculated by plot (Brown's protocol) or grid point (nail method). Fuel consumption was used as the metric of response. The average change in fuel height or load for each fuel class in unburned control units was subtracted from the change in fuel height or load in corresponding

burn treatments in the same replicate to account for fuel changes in the absence of fire. Bulk density, quadratic mean diameter, specific gravity, and non-horizontal correction coefficients were chosen from representative values for the region and forest type (Ottmar and Andreu 2007; B. Buchanan, United States Forest Service, Roanoke, Virginia, USA, unpublished report). The degree and variability of surface fuel consumption as quantified by changes in woody fuelbed height (cm); 1-hr, 10-hr, and 100-hr woody fuel load (kg ha⁻¹); and litter and duff load (kg ha⁻¹) were compared between dormant and growing season burn treatments.

Fuel moisture was measured in situ for litter and 1-hr woody (pooled) as well as 10-hr woody fuels in the fire behavior plots on the day of burn prior to ignition. Grab samples for this purpose (approx. 20 g) were collected from each plot corner and center (origin/SW, NW, NE, SE, and center), with disturbance of the surface fuel bed minimized at sampling locations [(5) litter/1-hr woody and (5) 10-hr woody fuel samples per plot; n = 25 measurement units for each fuel class per treatment unit]. All samples were sealed in 946 mL bags and weighed in the lab upon unsealing (wet mass), dried to constant weight at 75 °C (48 hours) and re-weighed after drying (dry mass). Fuel weight measurements for this purpose were recorded to the nearest 0.01 g. Relative moisture content for these fuels (%) was calculated and averaged by plot. Moisture content for coarser fuels and duff was not measured, as these materials are generally not consumed under typical prescribed fire conditions in the region.

Temperature was recorded continuously in situ before, during, and after passage of flaming fronts on each burn day using thermocouple probes. Onset Computer Corporation (Bourne, MA, USA) HOBO Type K Thermocouple data loggers were programmed to log temperature at a 1 s interval throughout the burn day (recording period 9 hr 1 min 58 sec), which were then attached to Cole-Parmer Instrument Company Digi-Sense Type K thermocouple probes (Vernon Hills, IL, USA), packaged, and buried in the ground approximately 15 cm deep prior to ignition. Probes protruded aboveground (sheath length = 30.48 cm) and were oriented such that the tip (sheath diameter = 0.1016 cm) faced downward at a uniform height of 2.54-5.08 cm above the litter surface (Figure 3). Thermocouples were positioned to record temperatures at each grid point intersection within the subset of 5 fire behavior plots per unit coincident with nail measurements of litter and duff consumption (16 probes per plot; n = 80 measurement units per treatment unit). Data logger and probe packages were retrieved within 48 hours after deployment with temperature measurements subsequently downloaded from each device. Data from loggers showing abnormal temperature profiles uncharacteristic of passage of a flaming front (i.e. suggesting recording failure) were excluded from analyses.

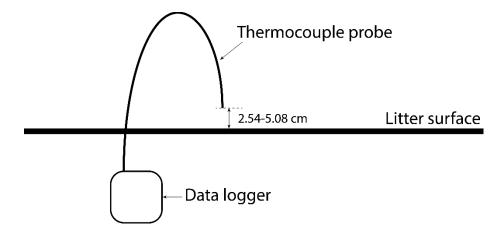


Figure 3. Diagram of thermocouple setup deployed at each plot grid point intersection. Data loggers were buried belowground in order to be shielded from the extreme temperatures of the fire aboveground. Probes attached to and extending from the data loggers were arranged with the tip at a uniform height and orientation above the litter surface.

Metrics of fire behavior were derived from thermocouple temperature profiles, calculated via different approaches and thresholds using an automated script in MATLAB R2020a Update 5 (MathWorks 2020). Following initial comparisons of these metrics, the time integral of absolute temperature above 60 °C (ABS60 approach) was chosen as the representative thermocouple heating metric relative to fire intensity for subsequent analysis. The time integral of temperature is the Riemann sum approximation of the product of time step and temperature, representing both the relative degree and residence time (i.e. "dose") of fire-induced heating experienced at a thermocouple probe tip. A threshold of 60 °C was chosen as the temperature at or above which thermocouple recordings would not only represent ambient heating, but a level of heating reached as a result of contact with the flaming front (Dickinson and Johnson 2004, Bova and Dickinson 2008). Temperature thresholds were also distinguished by their relative sensitivity in predicting surface fuel consumption during and after passage of a flaming front. The degree and variability of time-integrated thermocouple heating (ABS60 approach: JABS60; °C s) as well as the relationship between pooled litter and duff consumption (nail method; kg ha-1) vs. JABS60 at plot grid point intersections (aggregated as plot averages) were compared between dormant and growing season burn treatments.

Bole char height, an estimate of flame length related to thermocouple temperatures, was measured on hardwood tree species (e.g. *Quercus* spp., *Acer* spp., *Liriodendron tulipifera*) at all plot grid point intersections within burn units (Pomp et al. 2008). Measurements of bole char height were taken on the nearest charred bole (2.54 cm precision) within 3.05 m of each grid point (16 points per plot; n = 320 measurement units per treatment unit). Plot averages were obtained from these measurements. Bole char heights likely underestimated true flame length (Cain 1984) and were not measured on yellow pines [e.g. pitch pine (*Pinus rigida* Mill.) or shortleaf pine (*Pinus echinata* Mill.)] due to the increased likelihood of fire spread on the bark of these trees irrespective of surface flame heights.

Meteorological conditions represented by solar radiation, wind velocity, air temperature, fuel temperature, and relative humidity (RH) were gathered ex situ from the nearest Remote Automatic Weather Station (RAWS) at similar elevation to each treatment unit (MesoWest 2019). Weather information for each burn day was derived from the Andrew Pickens (Station ID: WLHS1), Tallulah (Station ID: TULG1), and Chattooga (Station ID: CHGG1) stations in northwestern South Carolina and northeastern Georgia. These weather stations were located within 21 km of corresponding burn locations. Solar radiation was summed and remaining variables were averaged between 08:00 and 19:59 local time, adjusted relative to daylight savings time clock forward dates on March 11, 2018 and March 10, 2019 (12 measurements of each variable at 1-hr increments on the hour). Additionally, the reported Keetch-Byram Drought Index (KBDI) was gathered for each corresponding burn day, accessed through the Weather Information Management System (WIMS) (2019). The degree and variability of both meteorological conditions (RAWS/WIMS) and fuel moisture (grab samples) on burn days were quantified for total solar radiation (KW-hr/m2), air temperature (°C), fuel temperature (°C), wind speed (m/s), RH (%), KBDI, pooled litter and 1-hr woody fuel moisture (%), and 10-hr woody fuel moisture (%) to compare between dormant and growing season burn treatments.

Topographic variables were derived from a digital elevation model (DEM) in a geographic information system (GIS) to evaluate topographic effects on fire behavior. A DEM

covering the study area was downloaded as part of the National Elevation Dataset from the U.S. Geological Survey's The National Map Viewer at a spatial resolution of 1/9 arc-second and transformed to a Universal Transverse Mercator (UTM) Zone 17 projected coordinate system (3.18 m cell size) (Esri 2019). The DEM had pits removed using TauDEM and was clipped to the necessary extent for analysis in ArcGIS Desktop 10.7.1 (Tarboton 2015, Esri 2019). Each index variable was normalized to a scale of 0-1 using the Raster Calculator tool and extracted using the Extract Multi Values to Points tool (Esri 2019).

Topographic Position Index (TPI) was used to quantify slope position, based on the relative difference between a given point's elevation and the average elevation of its surrounding terrain within a defined window (Guisan et al. 1999, De Reu et al. 2013). Lower values represented more sheltered parts of the landscape whereas higher values represented greater exposure. A rectangular window of 1000 m x 1000 m was chosen to define the focal area, with its average elevation subtracted from each cell in the DEM using the ArcGIS Geomorphometry and Gradient Metrics Toolbox to derive TPI (Evans et al. 2014a, b; A. Evans, Texas A&M University, College Station, TX, USA, personal communication; Esri 2019). Heat Load Index (HLI) was used to quantify solar radiation as a function of aspect, further incorporating the effects of slope and latitude to linearize compass azimuth such that it ranges from the lowest values on northeast-facing slopes to the highest values on southwest-facing slopes (Beers et al. 1966, McCune and Keon 2002). HLI was derived from the DEM using the ArcGIS Geomorphometry and Gradient Metrics Toolbox (Evans et al. 2014b, Esri 2019). TPI and HLI were averaged by plot area and related to bole char height (m) as topographic predictors of fire behavior, compared between dormant and growing season burns by individual burns and treatment means.

Vegetation was sampled in each forest layer (understory, midstory, and overstory) before and after each burn to determine changes in response to treatment. Pre-burn vegetation measurements were taken within 1-2 growing seasons (2016-17) preceding each burn (2018-19). Post-burn vegetation measurements were taken in the second growing season (2019-20) following each burn. Visual evidence of the presence or absence of fire (y/n) was noted at grid point intersections, with a 50% threshold of grid points indicating the presence of fire used to qualify plot-level burn treatment effects.

Understory vegetation was defined as living plants < 1.37 m in height and was recorded following a modified Carolina Vegetation Survey (CVS) protocol (Peet, Wentworth, and White 1998). Quadrats (1 m²) were used to sample understory vegetation, centered at each of 9 subplots per plot (n = 1,620 measurement units). Plants within each quadrat were identified to species when possible. Individual woody plants were tallied at or above the root collar within life history (germinant, established, sprout) and height (< 10 cm, 10-50 cm, ≥ 50 cm) classes. Unique plants were assigned cover classes that represented the proportion of the quadrat that it covered: (1) 0-1%, (2) 1-2%, (3) 2-5%, (4) 5-10%, (5) 10-25%, (6) 25-50%, (7) 50-75%, (8) 75-100%. Cover classes were converted to the midpoint of the class range and transformed using an arcsine-square root transformation (Sokal and Rohlf 1995; McCune and Grace 2002).

Midstory vegetation was defined as woody stems ≥ 1.37 m in height and < 10 cm diameter at 1.37 m (breast height) above ground level. Overstory vegetation was defined as woody stems ≥ 1.37 m in height and ≥ 10 cm diameter at breast height (DBH). Midstory vegetation was sampled within 5 of 9 subplots (odd-numbered subplots #1, 3, 5, 7, 9) per plot (n = 900 measurement units), whereas overstory vegetation was sampled in the same odd-numbered subplots in 2 of the 3 treatment replicates (n = 600 measurement units). Live stems were

identified to species when possible. Individual midstory plants (shrubs and trees) were tallied within the following DBH classes: (1) < 3 cm, (2) 3-6 cm, and (3) 6-10 cm. DBH of overstory plants (shrubs and trees) was measured for each individual. Proportion of midstory cover, both for mountain laurel and total overall, and maximum height of mountain laurel, alive and dead, was visually estimated for each subplot. Midstory cover proportion was transformed using an arcsine-square root transformation.

Plants were identified following the U.S. Department of Agriculture (USDA) Natural Resources Conservation Service (NRCS) PLANTS Database. Individual plants (typically species) were assigned to a functional group based on growth habit according to the PLANTS Database. Additional groups were defined using combinations of growth habits: herb (form, graminoid) and woody (shrub, tree, vine). Among trees, hickory included *Carya* spp., mesophytic hardwood was assigned according to genera and species listed by Nowacki and Abrams (2008), red oak (*Quercus* spp.) included *Q. coccinea*, *Q. falcata*, *Q. marilandica*, *Q. rubra*, and *Q. velutina*, white oak (*Quercus* spp.) included *Q. alba*, *Q. montana*, and *Q. stellata*, white pine included *Pinus strobus*, yellow pine (*Pinus* spp. subgenus Diploxylon) included *P. echinata*, *P. pungens*, *P. rigida*, *P. taeda*, and *P. virginiana*, and other included all other trees.

Plant functional group response variables were aggregated (summed or averaged) across subplots by plot (sample unit), with paired absences excluded for calculating Δ response values from pre- to post-treatment. For comparison of treatment effects on plant density, count data were transformed using a logarithmic transformation. (Anderson et al. 2006).

Species richness and proportionate measures of alpha (α), gamma (γ), and beta (β) diversity were calculated for plots, treatment units, and overall. Species richness was calculated by plot as mean plant richness. α -diversity (proportionate) was calculated by plot as the H' Shannon-Wiener index of diversity. Both species richness and H' were quantified overall and by plant functional group. γ -diversity was calculated as the total plant species richness by treatment unit and overall. β -diversity, representing the degree of compositional separation between plots, was calculated both as β W (Whittaker's beta) as well as β D (half changes), based on presence-absence and quantitative data, respectively (McCune and Grace 2002). Changes in diversity values from pre- to post-treatment (Δ) were analyzed as treatment effects.

Proportion of forest canopy cover was estimated to quantify the relative degree of understory light availability, using a spherical densiometer. The difference between post- and pre-treatment canopy cover proportion (Δ) was used as the metric of response.

Statistical analyses

A statistical model was developed that related the means of the continuous dependent variables to the treatments. Model effects included treatment (fixed), replicate (random), replicate crossed with treatment (random), and/or plot nested within treatment and replicate (random). Analysis of variance (ANOVA) techniques were used to evaluate the model terms and specifically test for treatment effects. For some variables the model residuals did not follow a normal distribution with stable variance across treatments, and therefore either a Kruskal-Wallis rank-based ANOVA (Boos and Brownie 1992) or a generalized linear model with an exponential distribution was used to test the treatment effect on responses.

A statistical model was also developed that related response variability to the treatments. Response variability was quantified as the coefficient of variation (CV). Model effects for this model included treatment (fixed) and/or replicate (random). Either a Wilcoxon rank sum test

(Mann-Whitney U test) or a generalized linear model with an exponential distribution was used to test the treatment effects on the response CVs.

Ordinary least squares regression modeling was used to estimate the slope and associated root mean square error (RMSE) between selected pairs of response variables within each treatment unit. A log transformation was used on heavily-skewed distributions when estimating the bivariate relationships. The slopes were included in a statistical model to relate to the treatments including model effects of treatment (fixed), replicate (random), and replicate crossed with treatment (random). A one-way ANOVA was used to test for the treatment effect in this model. The RMSEs were related to treatments with a statistical model including treatment (fixed) and replicate (random) only, also with a one-way ANOVA used to test for the treatment effect.

Across all models of treatment effects, response variable observations were aggregated at different levels with the overall objective of producing independent observations to be used in the model analyses. Statistical significance was evaluated either at the $\alpha=0.05$ level (non-ranked values) or $\alpha=0.10$ level (ranked values). All statistical calculations and figures were made using the latest versions of JMP Pro (up to v. 15.1.0) and RStudio Desktop (up to v. 1.4.1103) in the R (up to v. 4.0.5) programming language and software environment (SAS 2019, R Core Team 2021, RStudio 2021).

Relative changes in understory and midstory community composition in relation to treatments and environmental variables were assessed using nonmetric multidimensional scaling (NMDS). NMDS, a non-parametric and unconstrained ordination method, uses ranked distances to find the configuration of a specified number of dimensions (axes) relating site and species dissimilarities with minimum departure from monotonicity in its solution (Clarke 1993). Standardized species importance values (IV) representing relative abundance were used to calculate distance measures for the NMDS using the Bray-Curtis coefficient, a proportion coefficient equivalent to Sørensen similarity for quantitative data (Bray and Curtis 1957; Faith et al. 1987; McCune and Grace 2002). Euclidean distance was used for calculating environmental gradient distances for correlation with ordination axes. Procrustes analysis was used in comparing iterative solutions to determine convergence, with the final configuration rotated such that the first axis explained the greatest variance (Oksanen et al. 2019). To depict the results of the NMDS, sites (plots) were plotted in ordination space with change vectors overlaid indicating the average movement of plots by the centroid of plot points of each treatment by sampling period from pre- to post-treatment.

NMDS ordination configurations were related to environmental variables according to sampling period relative to application of treatment: elevation, TPI, HLI, and canopy cover (pretreatment) or elevation, TPI, HLI, dNBR, bole scorch height, Δ litter load, and Δ canopy cover (post-treatment). Environmental variable correlations with ordination axes were quantified as direction cosines of vectors, with the strength of the correlation expressed as a squared coefficient (r2). Explanation of changes in community assemblages were assessed according to combinations of environmental variables with the strongest correlation with species dissimilarities using Spearman's rank correlation coefficient (ρ). All multivariate community analyses were performed using RStudio in the R programming language and software environment (2020; R Core Team 2020). Functions included within the vegan package were used to produce the NMDS ordination and relate environmental variables to community configurations (Oksanen et al. 2019).

Results

Meteorology, fuel moisture, and proportion of plot area burned

The early growing season was characterized by greater solar radiation, warmer air temperatures and warmer fuels, relative to the dormant season. While air temperatures were cooler in the dormant season, they were more variable. This, however, did not translate to greater variation in fuel temperatures in the dormant season. Other meteorological parameters (wind speed, relative humidity, KBDI) did not significantly differ between seasons. Woody fuel moisture, for both 1-hour and 10-hour lag classes, was greater in the dormant season – but variation in fuel moisture did not vary between seasons (Table 3). The proportion of plot area burned was significantly greater, and less variable, in early growing season burns than in dormant season burns (Figure 4), with burned area correlating with fuel moisture (Figure 5).

Table 3. Summary of statistical comparisons of meteorological conditions from Remote Automatic Weather Stations (RAWS) or as reported in the Weather Information Management System (WIMS) and fuel moisture collected in the field (grab samples) on burn days by variable and burn treatment. Statistical analyses were performed using a non-parametric Kruskal-Wallis rank-based standard least squares ANOVA aggregated by plot (grab samples) or unit (RAWS/WIMS) with fixed effect of treatment and random effects of replicate and/or replicate crossed with treatment (response) or fixed effect of treatment and random effect of replicate (variability of response). Response variables include both the mean (\pm standard error) and coefficient of variation (CV; %). Tests with statistical significance (α = 0.10) are reported in boldface.

Response variable (* α = 0.10)	Burn treatment	Mean (± SE)	CV (%)
Meteorological condi	tions (RAWS	/WIMS)	
Total solar radiation [KW-hr/m ²]	DS	5.4 (± 0.8)	n/a
Mean: $F_{1, 2.4} = 7.24$, $P = *0.09$	GS	$6.7 (\pm 0.5)$	n/a
Air temperature [°C]	DS	10.6 (± 1.8)	48.4
Mean: $F_{1, 2.0} = 12.00$, $P = *0.07$ CV: $F_{1, 3.2} = 10.07$, $P = *0.05$	GS	21.7 (± 2.3)	21.3
Fuel temperature [°C]	DS	14.1 (± 2.8)	59.9
Mean: $F_{1, 1.8} = 36.07$, $P = *0.03$ CV: $F_{1, 1.5} = 9.96$, $P = 0.12$	GS	26.0 (± 2.2)	32.2
Wind speed [m/s]	DS	$1.5~(\pm~0.3)$	50.6
Mean: $F_{1, 2.4} = 0.54$, $P = 0.53$ CV: $F_{1, 3.2} = 0.88$, $P = 0.41$	GS	$1.6 (\pm 0.4)$	34.1
Relative humidity (RH) [%]	DS	27.2 (± 1.4)	49.4
Mean: $F_{1, 3.2} = 0.38$, $P = 0.58$ CV: $F_{1, 2.6} = 0.07$, $P = 0.81$	GS	31.4 (± 3.1)	40.7
Keetch-Byram Drought Index (KBDI)	DS	23.8 (± 12.6)	n/a
Mean: $F_{1, 2.8} = 2.51$, $P = 0.22$	GS	61.7 (± 13.4)	n/a

Fuel moisture	(grab sample	es)	
Litter and 1-hr woody [%]	DS	39.2 (± 6.3)	36.0
Response: $F_{1, 2.0} = 71.08$, $P = *0.01$ Variability: $F_{1, 2.4} = 3.75$, $P = 0.17$	GS	17.9 (± 2.7)	27.1
10-hr woody [%]	DS	38.9 (± 8.0)	39.6
Response: $F_{1, 2.6} = 9.79$, $P = *0.06$ Variability: $F_{1, 3.2} = 1.83$, $P = 0.26$	GS	14.6 (± 1.0)	20.9

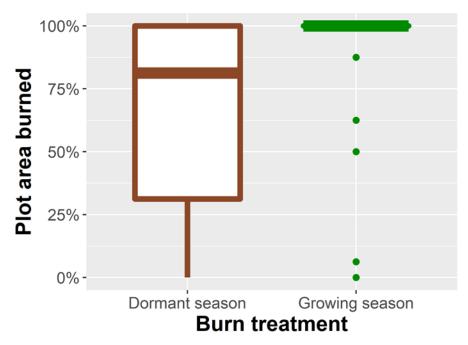


Figure 4. Boxplot of proportion of plot area burned (y-axis; %) by burn treatment (x-axis). Proportions were calculated based on the number of grid points indicating evidence of fire presence per plot.

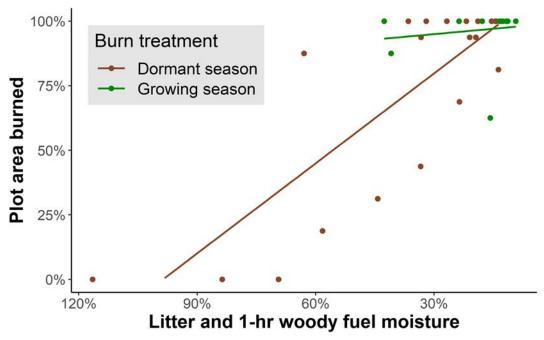


Figure 5. Scatterplot with linear regression of proportion of plot area burned (y-axis; %) vs. pooled litter and 1-hr woody fuel moisture (x-axis, reversed; %) in subset of fire behavior plots by burn treatment (series). Proportions were calculated based on the number of grid points indicating evidence of fire presence per plot.

Time-integrated heating and fuel consumption

Time-integrated thermocouple heating (JABS60) was more than 5x greater in the early growing season than in the dormant season and was also more variable (Figure 6). This pattern was largely driven by an increase in heating from fire midday and onward (Figure 7).

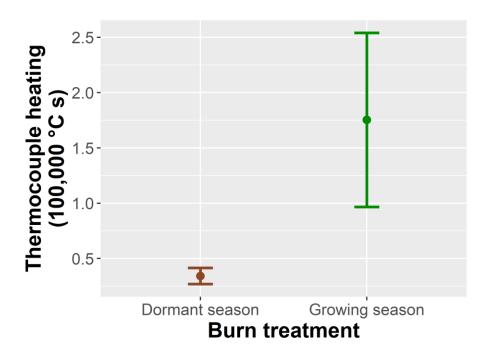


Figure 6. Plot of means of the time integral of thermocouple probe temperature (ABS60 approach) with error bars representing associated standard error (y-axis; $^{\circ}C$ s) by burn treatment (x-axis).

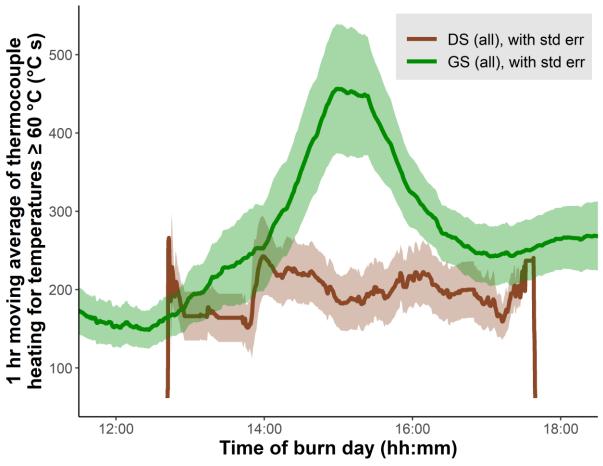


Figure 7. Plot of 1-hour, centered rolling mean (moving average) of the time integral of thermocouple probe temperature (ABS60 approach) (y-axis; °C s) vs. time of day (x-axis; hh:mm), by burn treatment from 11:30 am – 6:30 pm on burn days. Time of day was adjusted to account for daylight savings time clock forward dates in March 2018 and March 2019. Series include error bars (shaded area) representing associated standard error around the mean.

Fuel consumption

Woody fuelbed height and 1-hr, 10-hr, and 100-hr woody fuel consumption as measured using Brown's Planar Intercept Method were not significantly different between burn treatments. Likewise, using the nail method, litter consumption was not significantly different between burn treatments. While mean differences were not statistically different between treatments, there was greater variability in the change in woody fuelbed height and litter consumption in dormant season burns. However, duff consumption (nails) was significantly greater in growing season burns, with no measurable duff consumption was observed in dormant season burns (Table 4). Slope of the linear line of best fit between pooled litter and duff consumption and log-transformed JABS60 did not differ significantly between burn treatments, nor was there a difference in the root mean squared error (RSME) between treatments.

Table 4. Summary of statistical comparisons of fuel consumption by sampling protocol, fuel class, and burn treatment. Statistical analyses were performed using a non-parametric Kruskal-Wallis rank-based standard least squares ANOVA aggregated by plot with fixed effect of treatment and random effects of replicate, replicate crossed with treatment, and plot nested within treatment and replicate (response) or fixed effect of treatment and random effect of replicate (variability of response). Response variables

include both the mean (\pm standard error) and coefficient of variation (CV; %). Tests with statistical significance (α = 0.10) are reported in boldface.

Response variable (* α = 0.10)	Burn treatment	Mean (± SE)	CV (%)
Woody fuel cor	sumption (Br	rown 1974) [Δ]	
Woody fuelbed height [cm]	DS	5.0 (± 2.4)	629.2
Mean: $F_{1, 2.2} = 0.30$, $P = 0.63$ CV: $F_{1, 2.0} = 23.88$, $P = *0.04$	GS	3.9 (± 3.5)	256.9
1-hr woody [kg ha ⁻¹]	DS	66.5 (± 231.3)	83.7
Mean: $F_{1, 2.1} = 0.34$, $P = 0.61$ CV: $F_{1, n/a} = 0.00$, $P = n/a$	GS	217.2 (± 133.1)	400.9
10-hr woody [kg ha ⁻¹]	DS	298.6 (± 870.1)	141.3
Mean: $F_{1, 3.1} = 0.03$, $P = 0.86$ CV: $F_{1, 3.2} = 4.19$, $P = 0.13$	GS	296.3 (± 323.0)	627.4
100-hr woody [kg ha ⁻¹]	DS	4,160.0 (± 2,691.6)	128.0
Mean: $F_{1, 2.7} = 0.41$, $P = 0.57$ CV: $F_{1, 2.8} = 0.29$, $P = 0.63$	GS	2,701.4 (± 1,075.9)	271.3
Litter and duff co	onsumption (r	nail method) $[\Delta]$	
Litter [kg ha ⁻¹]	DS	2,664.6 (± 372.9)	94.4
Mean: $F_{1, 3.1} = 3.34$, $P = 0.16$ CV: $F_{1, 2.5} = 27.17$, $P = *0.02$	GS	4,365.0 (± 394.0)	41.1
Duff [kg ha ⁻¹]	DS	0.0 (± 0.0)	n/a
Mean: $F_{1, 2.0} = 11.34$, $P = *0.08$ CV: $F_{0, 0.0} = n/a$, $P = n/a$	GS	135.6 (± 113.7)	n/a

Topographic effects on fire behavior

Heat load index and bole char height were positively correlated. While the slope of this regression was steeper in dormant season burns compared to growing season burns (2.2 vs. 1.4), these differences were not statistically significant. Likewise, there were no statistically significant treatment effects for root mean squared errors or proportion of variance. A summary of bivariate comparisons of bole char height vs. topographic position and heat load indices by unit and treatment can be found in Figure 8.

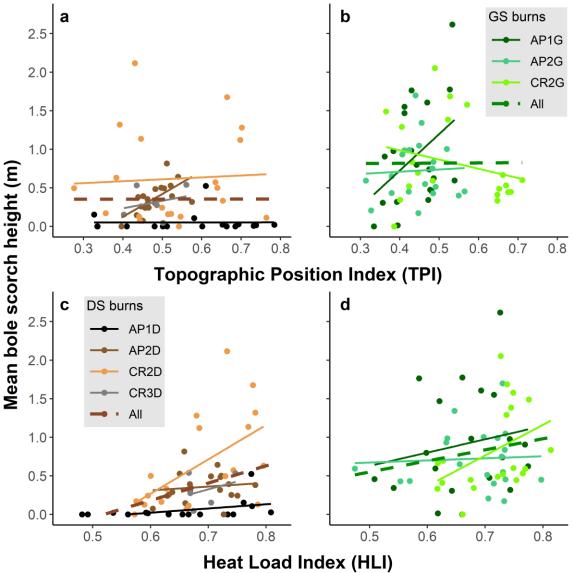


Figure 8. Scatterplots with linear regressions of mean bole char height (y-axis; m) vs. landscape indices Topographic Position Index (TPI) and Heat Load Index (HLI) (x-axis) by burn treatment (columns) and index (rows) for all plots in each unit (series). Top row, left column shows mean bole char height vs. TPI for dormant season burns (a), top row, right column shows mean bole char height vs. TPI for growing season burns (b), bottom row, left column shows mean bole char height vs. HLI for dormant season burns (c), and bottom row, right column shows mean bole char height vs. HLI for growing season burns (d).

Vegetation Cover and Density

Understory

Nearly all understory growth habits, tree groups, and species of management interest increased in cover during the study period – regardless of treatment. There were no significant treatment effects (all P > 0.05 or n/a). (Figure 9).

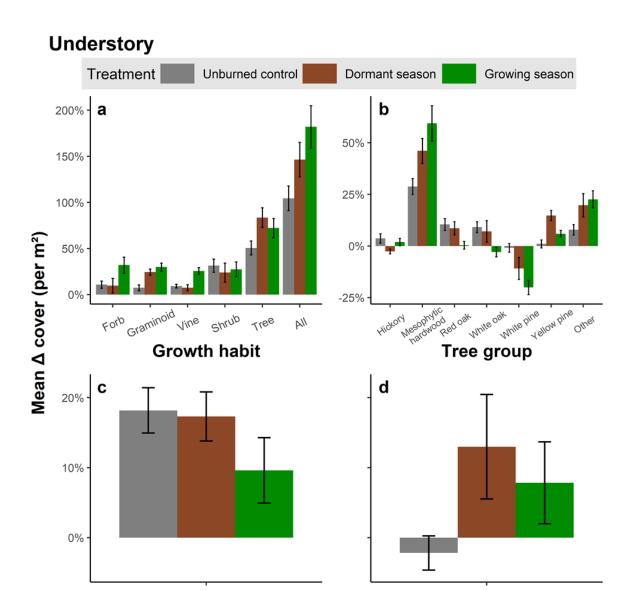


Figure 9. Summary of treatment effects on understory vegetation cover analyzed using a one-way ANOVA followed by Tukey's test: (a) all by growth habit, (b) trees by group, (c) red maple (Acer rubrum), and (d) mountain laurel (Kalmia latifolia). Response variables represent absolute changes and are summed by plot (sample unit; $9 \, m^2$) across individual subplot quadrats. Group means may not equal the sum of subgroup means due to the exclusion of paired absences.

Kalmia latifolia

Acer rubrum

Similar to understory cover, there were increases in understory stem density for all growth habits. There were no significant differences between treatments (all P > 0.05) (Figure 10). However, when broken out into life history categories, there were significantly more tree sprout stems in the growing season ($+17,191 \pm 2,207 \, \text{ha}^{-1}$) and dormant season treatments ($+16,869 \pm 2,530 \, \text{ha}^{-1}$) vs. unburned controls ($+1,833 \pm 607 \, \text{ha}^{-1}$) (P = 0.01). There were no other significant treatment effects for change in understory density of woody stems by growth habit and life history (all P > 0.05 or n/a) (Figure 11).

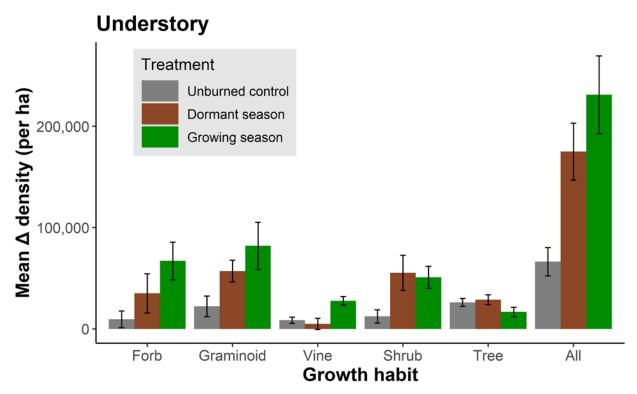


Figure 10. Summary of treatment effects on all understory vegetation density by growth habit analyzed using a one-way ANOVA followed by Tukey's test. Error bars represent standard error associated with each treatment and letters represent significant differences between treatments. Response variables represent absolute changes and are summed by plot (sample unit; $9 \, m^2$) across individual subplot quadrats. Group means may not equal the sum of subgroup means due to the exclusion of paired absences.

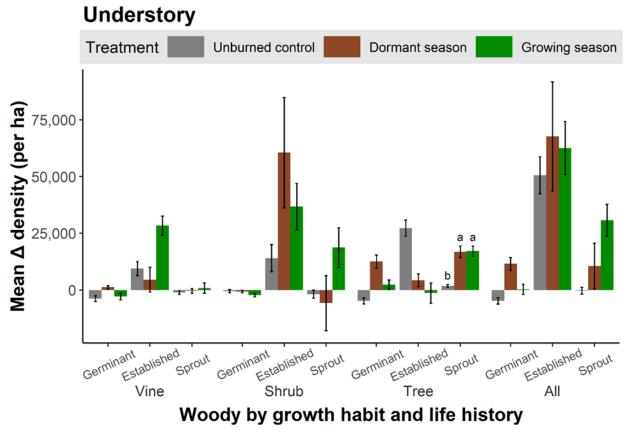


Figure 11. Summary of treatment effects on woody understory vegetation density by growth habit and life history analyzed using a one-way ANOVA. Response variables represent absolute changes and are summed by plot (sample unit; 9 m^2) across individual subplot quadrats. Group means may not equal the sum of subgroup means due to the exclusion of paired absences. Treatment means with different lower-case letters were statistically different at $\alpha = 0.05$.

When broken out into understory tree groups and their life history categories, there were no significant treatment effects for hickories, red oaks, white oaks, white pines or yellow pines (all P > 0.05 or n/a). However, there were the increase in the density of mesophytic hardwood sprouts was significantly greater in the growing season (+13,026 ± 2,107 ha⁻¹) and dormant season treatment (+13,065 ± 2,173 ha⁻¹) vs. unburned controls (+1,176 ± 551 ha⁻¹) (P = 0.02). Additionally, in the "other trees" category, the increase in total understory stems was significantly greater in the growing season treatment (+6,914 ± 1,351 ha⁻¹) vs. both the dormant season treatment (+2,049 ± 1,156 ha⁻¹) and the unburned controls (+1,206 ± 1,432 ha⁻¹) (P = 0.01) (Figure 12). This treatment effect was driven mostly by sourwood (*Oxydendrum arboreum* (L.) DC.), and black locust (*Robinia pseudoacacia* L.).

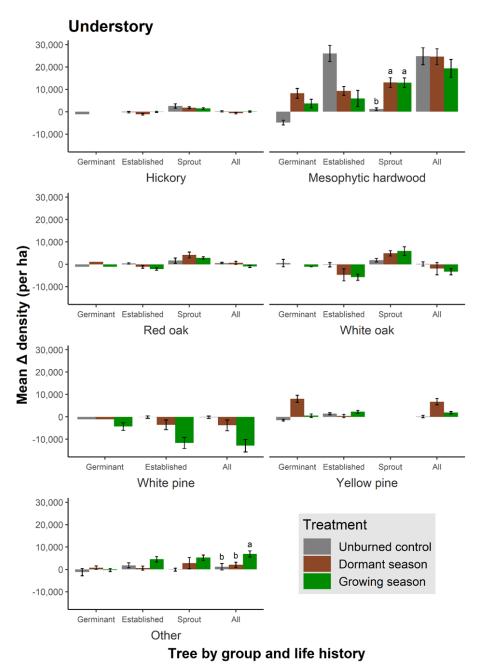


Figure 12. Summary of treatment effects on understory tree vegetation density by group and life history analyzed using a one-way ANOVA. Response variables represent absolute changes and are summed by plot (sample unit; 9 m^2) across individual subplot quadrats. Group means may not equal the sum of subgroup means due to the exclusion of paired absences. Treatment means with different lower-case letters were statistically different at $\alpha = 0.05$.

For other species of management interest, both the growing season and the dormant season treatments had significantly smaller changes in the density of established Acer rubrum stems (-9,581 \pm 1,881 ha⁻¹ and +3,000 \pm 1,788 ha⁻¹, respectively) relative to the unburned controls (+25,256 \pm 3,953 ha⁻¹) (P = 0.01). However the 2 burn treatments were not significantly different from one another. There were no other significant treatment effects any other life

history stage for *Acer rubrum*. Likewise, there were no significant treatment effects, for any life history stage, for *Kalmia latifolia* (P > 0.05 or n/a) (Figure 13).

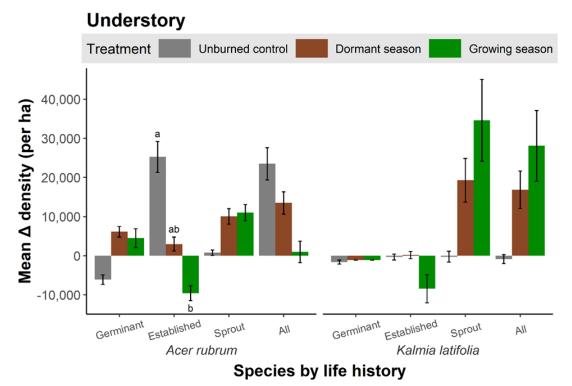


Figure 13. Summary of treatment effects on understory vegetation density of red maple (Acer rubrum) and mountain laurel (Kalmia latifolia) by life history analyzed using a one-way ANOVA. Response variables represent absolute changes and are summed by plot (sample unit; 9 m^2) across individual subplot quadrats. Group means may not equal the sum of subgroup means due to the exclusion of paired absences. Treatment means with different lower-case letters were statistically different at $\alpha=0.05$.

Midstory

Midstory cover, for both *Kalmia latifolia* and for all species pooled, decreased in all treatments (including control) during the study period. However, there were no significant differences between treatments (all P > 0.05) (Table 5).

Table 5. Summary of treatment effects on midstory vegetation cover analyzed using a one-way ANOVA followed by Tukey's test. Response variables are averaged by plot (sample unit; 500 m^2) across individual subplots.

Response variable (* $\alpha = 0.05$)	Treatment	Mean (± SE)	Tukey HSD
Cover [$\Delta \Sigma$ (proportion 0.01 n	n ⁻²)]		
W 1 · 1 · · · · · · · · · ·	С	-0.06 (± 0.09)	
Kalmia latifolia $F_{2,3.8} = 0.12, P = 0.89$	DS	$-0.24 (\pm 0.13)$	
	GS	$-0.22 (\pm 0.09)$	
Total	С	-0.27 (± 0.11)	
$F_{2,4.0} = 0.93, P = 0.47$	DS	$-0.95 (\pm 0.20)$	

GS

Midstory shrub density increased in the control treatment and decreased in the two burn treatments. The largest decrease was observed in the growing season burn treatment (-1,585 \pm 188 ha⁻¹), which was significantly different from both the dormant season treatment (-813 \pm 240 ha-1) and the unburned controls (+517 \pm 164 ha⁻¹) (P = 0.01). This treatment effect was largely driven by reductions in the <3 cm DBH size class. A similar, albeit less pronounced, effect was observed for midstory trees, where the growing season treatment had the greatest reduction (-889 \pm 133 ha⁻¹), followed by the dormant season treatment (-526 \pm 246 ha⁻¹) and unburned controls (-74 \pm 51 ha⁻¹). For midstory trees, the two burn treatments were not statistically different from eachother, but the growing season treatment was statistically different from the control (*P* = 0.02). Again, these differences were primarily driven by reductions in the smaller size classes (< 3 cm and 3-6 cm DBH) (Figure 14).

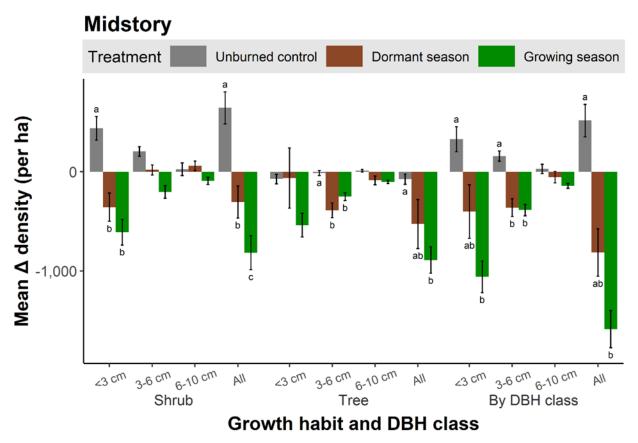


Figure 14. Summary of treatment effects on all midstory vegetation stem density by growth habit and DBH class analyzed using a one-way ANOVA followed by Tukey's test. Error bars represent standard error associated with each treatment mean and letters represent significant differences between treatments. Response variables represent absolute changes and are summed by plot (sample unit; $500 \, m^2$) across individual subplots. Group means may not equal the sum of subgroup means due to the exclusion of paired absences. Treatment means with different lower-case letters were statistically different at $\alpha = 0.05$.

When broken out into midstory tree groups and their life history categories, there were no significant treatment effects for stem density of hickories, white pines or yellow pines (all P > 0.05 or n/a). For mesophytic hardwoods, the unburned control stayed relatively unchanged (-17±

38 ha⁻¹), whereas reductions were observed in both the growing season and dormant season burn treatments (-561 \pm 80 ha⁻¹ and -376 \pm 165 ha⁻¹, respectively). While the two burn treatments were not statistically different from eachother, the growing season treatment was statistically different from the unburned control (P = 0.01). These differences were largely driven by mortality patterns in the <3 cm and 3-6 cm DBH classes. Likewise for midstory red oaks, there was a modest reduction in the unburned controls (-5 \pm 11 ha⁻¹) and a significantly larger reduction in the growing season treatment (-74 \pm 22 ha⁻¹) (P = 0.04). Changes for the dormant season treatment (-59 \pm 37 ha⁻¹) were not significantly different from either the unburned control or the dormant season treatment. Modest changes were also observed for "other" midstory trees, with significant reductions in 3-6 cm DBH class observed in the growing season treatment (-55 \pm 12 ha⁻¹) relative to the unburned controls (+3 \pm 9 ha⁻¹) (P = 0.03). Neither treatment was significantly different from the dormant season treatment (-73 \pm 29 ha⁻¹) (Figure 15).

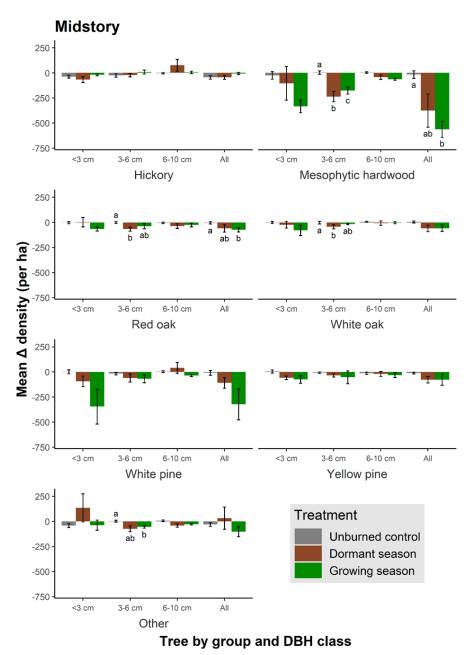


Figure 15. Summary of treatment effects on midstory tree vegetation density by group and DBH class analyzed using a one-way ANOVA. Response variables represent absolute changes and are summed by plot (sample unit; $500 \, \text{m}^2$) across individual subplots. Group means may not equal the sum of subgroup means due to the exclusion of paired absences. Treatment means with different lower-case letters were statistically different at $\alpha = 0.05$.

In the absence of fire, midstory density for *Acer rubrum* stayed relatively unchanged across size classes. However, there were significant reductions in total midstory *Acer rubrum* stem density in the growing season treatment, relative to all other treatments (-356 \pm 57 ha-1 vs - 219 \pm 69 ha⁻¹ and +15 ha⁻¹ \pm 31 ha⁻¹ in the dormant season and control treatments, respectively) (P < 0.01). In contrast with *Acer rubrum*, *Kalmia latifolia* midstory stem density increased in the absence of fire. In the growing season treatment, it decreased in all size classes, but was never

statistically different from the dormant season treatment. In the 0-3 cm DBH class, both the growing season and dormant season treatments were statistically different from the unburned control (-494 \pm 83 ha⁻¹ and -323 \pm 146 ha⁻¹ vs. +497 \pm 127 ha⁻¹, respectively) (Figure 16). Change in the maximum height of Kalmia latifolia was not significantly different between burn treatments (P = 0.49).

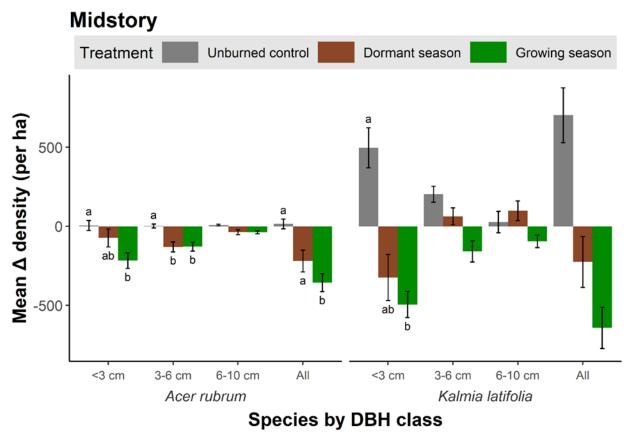


Figure 16. Summary of treatment effects on midstory vegetation density of red maple (Acer rubrum) and mountain laurel (Kalmia latifolia) by DBH class analyzed using a one-way ANOVA. Response variables represent absolute changes and are summed by plot (sample unit; 500 m^2) across individual subplots. Group means may not equal the sum of subgroup means due to the exclusion of paired absences. Treatment means with different lower-case letters were statistically different at $\alpha = 0.05$.

Overstory

In the absence of fire, stem density for overstory trees stayed constant or increased, depending on species or group. Reductions that were observed in both the growing season and dormant season treatments were not statistically significant (all P > 0.05 or n/a) (Figure 17).

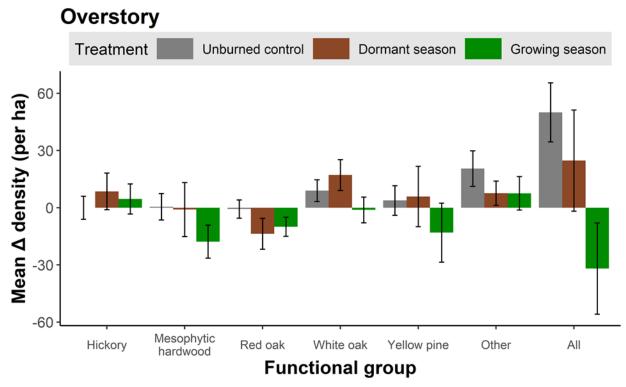


Figure 17. Summary of treatment effects on overstory vegetation density by functional group analyzed using a one-way ANOVA. Response variables represent absolute changes and are summed by plot (sample unit; 500 m²) across individual subplots. Group means may not equal the sum of subgroup means due to the exclusion of paired absences.

Species Richness, Diversity, and Overstory Cover

Understory

With the exception of shrubs in the unburned control, understory species richness generally increased in all treatments during the study period. However, there were no significant differences between treatments for any growth habit. Likewise for H, there were increases across all treatments – except for shrubs and trees in the unburned control – with no significant differences between treatments (all P > 0.05 or n/a) (Table 6). Likewise, change in γ , βW (Whittaker's beta), and βD (half changes) were not significantly different between burn treatments (P = 0.85, 0.21, and 0.11, respectively).

Table 6. Summary of treatment effects on understory species richness and α -diversity (H') analyzed using a one-way ANOVA. Response variables are aggregated by plot (sample unit; 9 m²) across individual subplot quadrats. Group means may not equal the sum of subgroup means due to the exclusion of paired absences.

Response variable (* α = 0.05)	Treatment	Mean (± SE)	Tukey HSD
Species richness [Δ]			
By growth habit			

-		
E. J.	C	$+1.07~(\pm~0.19)$
Forb $F_{2, 4.0} = 0.40, P = 0.70$	DS	$+1.36~(\pm~0.33)$
$\Gamma_{2,4.0} - 0.40, \Gamma - 0.70$	GS	$+1.89 (\pm 0.31)$
G	С	$+0.17~(\pm~0.08)$
Graminoid	DS	$+0.64~(\pm~0.17)$
$F_{2,3.6} = 2.57, P = 0.20$	GS	$+0.84~(\pm~0.12)$
	С	+1.24 (± 0.23)
Herb (forb, graminoid)	DS	$+2.00 (\pm 0.39)$
$F_{2, 4.0} = 0.70, P = 0.55$	GS	$+2.73~(\pm~0.35)$
	С	+0.22 (± 0.10)
Vine	DS	$+0.14~(\pm~0.19)$
$F_{2, 4.2} = 0.88, P = 0.48$	GS	$+0.52~(\pm~0.10)$
	С	-0.14 (± 0.11)
Shrub	DS	$+0.81~(\pm~0.21)$
$F_{2, n/a} = 1.39$	GS	$+0.91 (\pm 0.19)$
	С	+0.61 (± 0.27)
Tree	DS	$+0.78 (\pm 0.30)$
$F_{2, 4.4} = 0.03, P = 0.97$	GS	$+0.61 (\pm 0.31)$
	С	+0.69 (± 0.34)
Woody (vine, shrub, tree)	DS	$+1.72 (\pm 0.49)$
$F_{2, 4.1} = 0.49, P = 0.64$	GS	$+2.04 (\pm 0.43)$
H' (Shannon-Wiener index) [Δ]		
By growth habit		
	С	+0.29 (± 0.06)
Forb	DS	$+0.26~(\pm~0.08)$
	DS GS	+0.26 (± 0.08) +0.13 (± 0.07)
Forb F _{2, n/a} = 1.36	DS	+0.26 (± 0.08) +0.13 (± 0.07) +0.10 (± 0.08)
Forb $F_{2, n/a} = 1.36$ Graminoid	DS GS C DS	+0.26 (± 0.08) +0.13 (± 0.07) +0.10 (± 0.08) +0.16 (± 0.08)
Forb F _{2, n/a} = 1.36	DS GS C	+0.26 (± 0.08) +0.13 (± 0.07) +0.10 (± 0.08) +0.16 (± 0.08) +0.30 (± 0.07)
Forb $F_{2, n/a} = 1.36$ Graminoid $F_{2, 3.9} = 0.37, P = 0.71$	DS GS C DS GS	+0.26 (± 0.08) +0.13 (± 0.07) +0.10 (± 0.08) +0.16 (± 0.08) +0.30 (± 0.07) +0.25 (± 0.06)
Forb $F_{2, n/a} = 1.36$ Graminoid $F_{2, 3.9} = 0.37, P = 0.71$ Herb (forb, graminoid)	DS GS C DS GS C C DS	+0.26 (± 0.08) +0.13 (± 0.07) +0.10 (± 0.08) +0.16 (± 0.08) +0.30 (± 0.07) +0.25 (± 0.06) +0.25 (± 0.07)
Forb $F_{2, n/a} = 1.36$ Graminoid $F_{2, 3.9} = 0.37, P = 0.71$	DS GS C DS GS	+0.26 (± 0.08) +0.13 (± 0.07) +0.10 (± 0.08) +0.16 (± 0.08) +0.30 (± 0.07) +0.25 (± 0.06)
Forb $F_{2, n/a} = 1.36$ Graminoid $F_{2, 3.9} = 0.37, P = 0.71$ Herb (forb, graminoid) $F_{2, 3.1} = 0.01, P = 0.99$	DS GS C DS GS C C DS	+0.26 (± 0.08) +0.13 (± 0.07) +0.10 (± 0.08) +0.16 (± 0.08) +0.30 (± 0.07) +0.25 (± 0.06) +0.25 (± 0.07) +0.26 (± 0.06) +0.09 (± 0.04)
Forb $F_{2, n/a} = 1.36$ Graminoid $F_{2, 3.9} = 0.37, P = 0.71$ Herb (forb, graminoid) $F_{2, 3.1} = 0.01, P = 0.99$ Vine	DS GS C DS GS C DS GS C DS GS	+0.26 (± 0.08) +0.13 (± 0.07) +0.10 (± 0.08) +0.16 (± 0.08) +0.30 (± 0.07) +0.25 (± 0.06) +0.25 (± 0.07) +0.26 (± 0.06)
Forb $F_{2, n/a} = 1.36$ Graminoid $F_{2, 3.9} = 0.37, P = 0.71$ Herb (forb, graminoid) $F_{2, 3.1} = 0.01, P = 0.99$	DS GS C DS GS C DS GS C C C C C C C C C C C C C C C C C C	+0.26 (± 0.08) +0.13 (± 0.07) +0.10 (± 0.08) +0.16 (± 0.08) +0.30 (± 0.07) +0.25 (± 0.06) +0.25 (± 0.07) +0.26 (± 0.06) +0.09 (± 0.04)
Forb $F_{2, n/a} = 1.36$ Graminoid $F_{2, 3.9} = 0.37, P = 0.71$ Herb (forb, graminoid) $F_{2, 3.1} = 0.01, P = 0.99$ Vine $F_{2, 2.3} = 0.21, P = 0.83$	DS GS C DS GS C DS GS C DS GS	+0.26 (± 0.08) +0.13 (± 0.07) +0.10 (± 0.08) +0.16 (± 0.08) +0.30 (± 0.07) +0.25 (± 0.06) +0.25 (± 0.07) +0.26 (± 0.06) +0.09 (± 0.04) +0.04 (± 0.05)
Forb $F_{2, n/a} = 1.36$ Graminoid $F_{2, 3.9} = 0.37, P = 0.71$ Herb (forb, graminoid) $F_{2, 3.1} = 0.01, P = 0.99$ Vine $F_{2, 2.3} = 0.21, P = 0.83$ Shrub	DS GS C DS GS C DS GS C DS GS C C S GS	+0.26 (± 0.08) +0.13 (± 0.07) +0.10 (± 0.08) +0.16 (± 0.08) +0.30 (± 0.07) +0.25 (± 0.06) +0.25 (± 0.07) +0.26 (± 0.06) +0.09 (± 0.04) +0.04 (± 0.05) +0.11 (± 0.03)
Forb $F_{2, n/a} = 1.36$ Graminoid $F_{2, 3.9} = 0.37, P = 0.71$ Herb (forb, graminoid) $F_{2, 3.1} = 0.01, P = 0.99$ Vine $F_{2, 2.3} = 0.21, P = 0.83$	DS GS C DS GS C DS GS C DS GS C C C C C C C C C C C C C C C C C C	+0.26 (± 0.08) +0.13 (± 0.07) +0.10 (± 0.08) +0.16 (± 0.08) +0.30 (± 0.07) +0.25 (± 0.06) +0.25 (± 0.07) +0.26 (± 0.06) +0.09 (± 0.04) +0.04 (± 0.05) +0.11 (± 0.03) -0.02 (± 0.04)
Forb $F_{2, n/a} = 1.36$ Graminoid $F_{2, 3.9} = 0.37, P = 0.71$ Herb (forb, graminoid) $F_{2, 3.1} = 0.01, P = 0.99$ Vine $F_{2, 2.3} = 0.21, P = 0.83$ Shrub $F_{2, 4.0} = 2.09, P = 0.24$	DS GS C DS GS C DS GS C DS C DS GS C DS	+0.26 (± 0.08) +0.13 (± 0.07) +0.10 (± 0.08) +0.16 (± 0.08) +0.30 (± 0.07) +0.25 (± 0.06) +0.25 (± 0.07) +0.26 (± 0.06) +0.09 (± 0.04) +0.04 (± 0.05) +0.11 (± 0.03) -0.02 (± 0.04) +0.11 (± 0.06)
Forb $F_{2, n/a} = 1.36$ Graminoid $F_{2, 3.9} = 0.37, P = 0.71$ Herb (forb, graminoid) $F_{2, 3.1} = 0.01, P = 0.99$ Vine $F_{2, 2.3} = 0.21, P = 0.83$ Shrub $F_{2, 4.0} = 2.09, P = 0.24$ Tree	DS GS C DS	+0.26 (± 0.08) +0.13 (± 0.07) +0.10 (± 0.08) +0.16 (± 0.08) +0.30 (± 0.07) +0.25 (± 0.06) +0.25 (± 0.06) +0.26 (± 0.06) +0.09 (± 0.04) +0.04 (± 0.05) +0.11 (± 0.03) -0.02 (± 0.04) +0.11 (± 0.06) +0.26 (± 0.05)
Forb $F_{2, n/a} = 1.36$ Graminoid $F_{2, 3.9} = 0.37, P = 0.71$ Herb (forb, graminoid) $F_{2, 3.1} = 0.01, P = 0.99$ Vine $F_{2, 2.3} = 0.21, P = 0.83$ Shrub $F_{2, 4.0} = 2.09, P = 0.24$	DS GS C C C C C C C C C C C C C C C C C C	+0.26 (± 0.08) +0.13 (± 0.07) +0.10 (± 0.08) +0.16 (± 0.08) +0.30 (± 0.07) +0.25 (± 0.06) +0.25 (± 0.07) +0.26 (± 0.06) +0.09 (± 0.04) +0.04 (± 0.05) +0.11 (± 0.03) -0.02 (± 0.04) +0.11 (± 0.06) +0.26 (± 0.05) -0.06 (± 0.05)
Forb $F_{2, n/a} = 1.36$ Graminoid $F_{2, 3.9} = 0.37, P = 0.71$ Herb (forb, graminoid) $F_{2, 3.1} = 0.01, P = 0.99$ Vine $F_{2, 2.3} = 0.21, P = 0.83$ Shrub $F_{2, 4.0} = 2.09, P = 0.24$ Tree	DS GS C DS	+0.26 (± 0.08) +0.13 (± 0.07) +0.10 (± 0.08) +0.16 (± 0.08) +0.30 (± 0.07) +0.25 (± 0.06) +0.25 (± 0.07) +0.26 (± 0.06) +0.09 (± 0.04) +0.04 (± 0.05) +0.11 (± 0.03) -0.02 (± 0.04) +0.11 (± 0.06) +0.26 (± 0.05) -0.06 (± 0.05) +0.03 (± 0.05)
Forb $F_{2, n/a} = 1.36$ Graminoid $F_{2, 3.9} = 0.37, P = 0.71$ Herb (forb, graminoid) $F_{2, 3.1} = 0.01, P = 0.99$ Vine $F_{2, 2.3} = 0.21, P = 0.83$ Shrub $F_{2, 4.0} = 2.09, P = 0.24$ Tree $F_{2, 4.0} = 0.13, P = 0.88$	DS GS C DS GS GS C C DS GS	+0.26 (± 0.08) +0.13 (± 0.07) +0.10 (± 0.08) +0.16 (± 0.08) +0.30 (± 0.07) +0.25 (± 0.06) +0.25 (± 0.07) +0.26 (± 0.06) +0.09 (± 0.04) +0.04 (± 0.05) +0.11 (± 0.03) -0.02 (± 0.04) +0.11 (± 0.06) +0.26 (± 0.05) -0.06 (± 0.05) +0.03 (± 0.05) +0.04 (± 0.06)

Midstory

In contrast with the understory, midstory species richness generally decreased across treatments, but there were no significant treatment effects for either shrubs or trees (P > 0.05). Likewise, H' also decreased across treatments, with no significant treatment effects (P > 0.05). (Table 7).

Table 7. Summary of treatment effects on midstory species richness and α -diversity (H') analyzed using a one-way ANOVA. Response variables are aggregated by plot (sample unit; 500 m²) across individual subplots.

Response variable (* $\alpha = 0.05$)	Treatment	Mean (± SE)	Tukey HSD
Species richness [Δ]			
By growth habit			
Shrub $F_{2,3.9} = 2.15, P = 0.23$	C DS GS	0.00 (± 0.10) -0.19 (± 0.16) -0.45 (± 0.15)	
Tree $F_{2, 2.9} = 1.29, P = 0.40$	C DS GS	-0.92 (± 0.26) -1.50 (± 0.42) -1.91 (± 0.30)	
H' (Shannon-Wiener index) [A	Δ]		
By growth habit			
Shrub $F_{2, 3.6} = 1.63, P = 0.31$	C DS GS	-0.01 (± 0.03) -0.16 (± 0.06) -0.14 (± 0.06)	
Tree $F_{2, 3.0} = 6.30, P = 0.08$	C DS GS	-0.11 (± 0.03) -0.19 (± 0.06) -0.31 (± 0.06)	

Change in γ was not significantly different between burn treatments (P=0.44). However, Change in β W (Whittaker's beta) was significantly greater in the growing season treatment ($+1.12\pm0.13$) vs. unburned controls ($+0.11\pm0.20$) but was not significantly different from the dormant season treatment ($+0.28\pm0.18$) (P=0.04). Change in β D (half changes) was significantly greater in the growing season and dormant season treatments ($+0.28\pm0.08+0.20\pm0.04$, respectively) vs. unburned controls (-0.06 ± 0.03) (P<0.01).

Canopy cover

Overstory canopy cover increased in the absence of fire ($\pm 2.9\% \pm 3.2\%$) and decreased significantly in the 2 burn treatments ($\pm 5.5\% \pm 7.2\%$ and $\pm 4.0\% \pm 7.0\%$ in growing season and dormant season, respectively) (P < 0.01). The growing season and dormant season treatments were not significantly different (Figure 18).

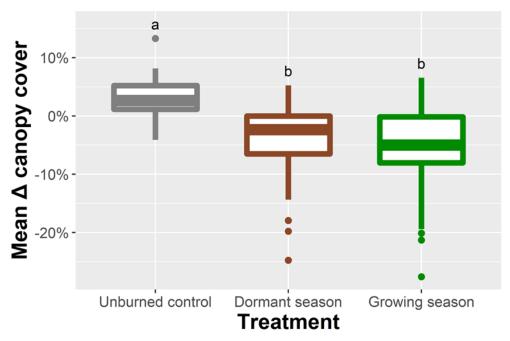


Figure 18. Comparison of change in canopy cover (%) by treatment. Treatment means with different lower-case letters were statistically different at $\alpha = 0.05$.

Ordination with environmental variables

Multivariate community ordination using NMDS of understory species IVs resulted in pre- and post-treatment final stress values of 0.25 and 0.26, respectively, with resolution on 2 axes after 755 and 20 iterations, respectively. For the pre-treatment NMDS ordination, elevation alone was the environmental variable with the strongest correlation with understory community configuration (ρ = 0.40). With elevation excluded, TPI and HLI together had the strongest correlation (ρ = 0.23). For the post-treatment NMDS ordination, elevation alone was the environmental variable with the strongest correlation with understory community configuration (ρ = 0.31). With elevation excluded, TPI, HLI, bole scorch height, and Δ litter load together had the strongest correlation (ρ = 0.21).

Using the same NMDS procedure, ordination of midstory species IVs resulted in pre- and post-treatment final stress values of 0.28, with resolution on 2 axes after 35 and 37 iterations, respectively. For the pre-treatment NMDS ordination, elevation alone was the environmental variable with the strongest correlation with understory community configuration (ρ = 0.43). With elevation excluded, TPI alone had the strongest correlation (ρ = 0.19). For the post-treatment NMDS ordination, elevation, dNBR, and Δ canopy cover together was the subset of

environmental variables with the strongest correlation with understory community configuration ($\rho = 0.34$). With elevation excluded, TPI, dNBR, bole scorch height, and Δ canopy cover together had the strongest correlation ($\rho = 0.25$) (Figure 19).

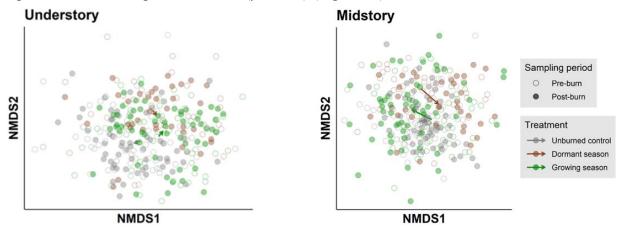


Figure 19. Plot of non-metric multidimensional scaling (NMDS) ordination results based on understory (left) and midstory (right) species importance values (IVs). Circles represent sites (plots) and arrows represent change vectors indicating plot movement from pre- to post-treatment by treatment.

Discussion

Fuels and Fire Behavior

This study examined factors of the fire environment related to season of burn to gain a better understanding of how these parameters influence prescribed fire behavior and first-order effects. Relating fire behavior and fire effects to environmental mechanisms representative of burning season may promote meaningful interpretations of prescribed fire seasonality for both scientists and managers (O'Brien et al. 2018, Hiers et al. 2020).

Following the winter solstice in the Northern Hemisphere, ambient temperatures begin to increase as a result of increasing photoperiod from a more direct sun angle (Schroeder and Buck 1970). Reflecting this trend and supporting our hypothesis, diurnal solar radiation and mean ambient temperatures (both of air and fuel) were greater, and fuels were drier, in early growing season burns. Warmer, precipitation-free periods typically increase in frequency by late winter in the Southeast, with favorable atmospheric conditions for fire spread following passage of cold fronts (Robbins and Myers 1992, Chiodi et al. 2018). Other key prescription window parameters influencing fire behavior (wind speed, RH, and KBDI) did not vary by season of burn, however. Consistently low KBDI values reflect long term trends in the southern Appalachians for the period of January-April in which burns were conducted for this study (Keetch and Byram 1968). These results suggest that seasonal variability of prescribed fire behavior in southern Appalachian forests before complete overstory leaf-out may be influenced by solar radiation and fuel moisture more so than other environmental conditions that remained similar between seasons.

Patterns of the proportion of plot area burned showed significant differences that may provide evidence for seasonal effects on fire spread. While the area and topographic heterogeneity of dormant season burn units (mean area = 363.5 ha) was greater than that of early

growing season burn units (mean area = 190.6 ha), proportion of plot area burned was significantly greater in the growing season than in the dormant season. Observed patterns indicate that ignition probability is greater in the early growing season, but do not necessarily suggest that other fire behavior parameters will be more uniform when prescribed burns are implemented in this season. Variable fire behavior in the dormant season created a mosaic of burned and unburned areas, which may be a desirable outcome if habitat heterogeneity is an objective.

Temperatures recorded by thermocouple probes are related to fireline intensity and were used in this study as an index of heating (Kennard et al. 2005, Bova and Dickinson 2008). Both the degree and variability of time-integrated thermocouple heating were greater in early growing season burns than in dormant season burns. Similar to a nearby study with burns conducted at the same time of year, differences in ambient air temperature by season of burn likely influenced fire behavior (Keyser et al. 2019). Less additional heat would be required for combustion to occur with warmer air in the early growing season.

Temporal variation in the relative amount and duration of heating experienced throughout the burn day also differed by season of burn. Dormant season burns were more limited in their distribution of periods of high levels of thermocouple heating (\geq 60 °C s), with early growing season burns having such periods starting before and continuing after those of dormant season burns. These patterns suggest that surface temperatures in a prescribed fire respond more positively to the warmest and driest part of the day in the mid-late afternoon in the early growing season than those in dormant season burns. Even if recent precipitation saturates surface fuels to a similar degree as in the dormant season, greater solar radiation in the early growing season can dry forest fuels more rapidly, which may have implications for fire effects (Byram and Jemison 1943).

There was little indication based on the results of our study that surface fuel consumption in areas where fire spread varied by season of burn. Greater proportions of plot area were burned in the early growing season, but for plots with at least 50% of grid points indicating fire presence, fuel load reduction largely did not differ between burn treatments. Among fuel classes measured, only duff consumption was significantly greater in early growing season burns, which may reflect greater duff fuel availability from drier conditions at the fuelbed surface (Ferguson et al. 2002, Waldrop et al. 2010). A relationship between fuel moisture and consumption would not explain the lack of seasonal differences observed for litter and woody fuel consumption, however. We further hypothesized that the variability of surface fuel consumption would be greater in early growing season burns than in dormant season burns, but our results do not support this. Rather, while variability in woody fuel consumption (1-hr, 10-hr, and 100-hr) did not differ by season of burn, litter consumption and woody fuelbed height reduction were more variable in dormant season burns. With less plot area burned, this result in the dormant season reflects a more bifurcated outcome at this time of year of either (a) low-moderate fuel consumption or (b) no consumption as a result of no ignition.

Our findings of surface fuel consumption ran contrary to our hypothesis as we expected warmer and drier conditions in the early growing season to result in higher levels of surface fuel consumption. In contrast, another study in the southern Appalachians found higher KBDI as a strong predictor of increased fuel consumption (Jenkins et al. 2011). The range of dates of burn and KBDI in different seasons was much greater in that study than ours, however, which may limit study comparisons. The fact that greater heat pulses did not correspond with increased surface fuel consumption in our study suggests that moisture levels did not limit combustion in

either season. Indeed, in longleaf pine savannas of the Coastal Plain, a study of fire regime dynamics over several years found that fuel consumption did not correlate with eight intraannual periods dispersed throughout the year, but fire intensity varied considerably as a function of rate of spread (Glitzenstein et al. 1995). Higher solar angles and lower fuel moisture in the early growing season likely allowed fire to spread to more variable landscape positions and burn at higher temperatures than in the dormant season while maintaining similar levels of fuel consumption.

Vegetation

Past studies of the effects of fire seasonality on vegetation in the southern Appalachians have demonstrated similar effects of burning in different seasons. For a single species [shortleaf pine (*Pinus echinata* Mill.)], season of burn did not affect seedling survival, though sprout height became greater with burning earlier (April) rather than later (July, November) in the year (Clabo and Clatterbuck 2019). At the stand scale (≤ 20 ha), fire applied in parts of the dormant (March) and growing (April, October) seasons indicated few significant differences of season of burn on changes in woody stem density (Keyse et al. McNab 2019; Vander Yacht et al. 2017). Response of understory vegetation in closed-canopy forests may be only marginally affected by surface fires in different seasons if there is no resultant increase in light availability (Alexander et al. 2008; Hutchinson et al. 2012). Further, changes in the relative abundance of different plant species within a community may be more sensitive to variability in fire behavior on a given burn day than burning in different seasons (Keyser et al. 2019).

The results of our study suggest that understory cover and density were largely unaffected by season of burn. Few significant treatment effects were detected that would indicate that understory plants of particular growth habits or in different life history stages responded differently to burns applied in different seasons. Contrary to our hypothesis, we did not find evidence to suggest that early growing season burns were more effective in increasing forb and graminoid abundance. While reductions in litter load may enhance understory germination, litter consumption did not significantly differ between season of burn treatments (Vaughan et al. in review). Some of the few significant differences in understory abundance between treatments were between the burn treatments and unburned controls, including stem density of both all tree sprouts and mesophytic hardwood tree sprouts. These results reflect the common observation of basal sprouting from midstory/overstory trees (Brose and Van Lear 2004; Elliott et al. 1999). Growing season burns, were, however, more effective than the other treatments in increasing the stem density of other trees such as sourwood, black locust and American holly (*Ilex opaca* Aiton). Trees in the "other" group often had divergent characteristics and therefore treatment differences observed may not reflect a functional response shared by most species within that group.

Growing season burns resulted in a decrease in the stem density of established red maple (*Acer rubrum* L.) in the understory relative to unburned controls, though not in comparison to dormant season burns. Changes in the abundance of established red maples as a result of burn treatments likely reflects both the mortality of stems present prior to the burn as well as the consumption of seeds by fire that would have become established in the growing seasons post-fire. Red maple is a dominant mesophytic competitor to the advance regeneration of oaks and hickories and germinates prolifically even under high shade (Walters and Yawney 1990; Abrams 1998; Hutchinson et al. 2008). In Eastern deciduous forests, red maple is among the earliest and most vigorous in initiating stem growth in the spring (Jacobs 1965). If red maples are

preferentially allocating resources to growth during this period, then this species may be more sensitive to disturbance in the early growing season (Trickett 2018). Nevertheless, while burning in the growing season was the most effective treatment in reducing established understory red maples, growing season burns did not reduce the density of germinant and sprout stems of this species nor were more effective in doing so than the other treatments. Therefore, changes in the abundance of understory red maple should continue to be monitored, particularly if reproductive red maples remain present in the overstory.

In contrast to the understory, the results of our study suggest that season of burn had many significant effects on the midstory. Growing season burns were more effective than the other treatments in reducing the stem density of midstory shrubs. Dormant season burns, in comparison, reduced shrub stem density to a lesser extent than growing season burns, whereas unburned controls saw an increase in shrub stem density. Burning in the dormant and/or growing season significantly reduced the stem density of red oaks in comparison to the unburned controls. Treatment response in the midstory may reveal which shrubs and trees are most susceptible to fire-induced mortality as a result of fire behavior more likely to occur in that season.

Growing season burns conducted in this study had higher levels of solar radiation, air temperature, and fuel temperature as well as lower fine fuel moisture than in dormant season burns (Vaughan et al. in review). Whereas wind speed, relative humidity (RH), and KBDI did not significantly differ by season of burn, time-integrated temperatures recorded by thermocouple probes during and after passage of flaming fronts were significantly higher in growing season burns than in dormant season burns. Accordingly, greater area was burned within growing season burn units than in units burned in the dormant season. Such variability in fire behavior on burn days suggests that mortality of woody stems may differ based on the extent, intensity, and severity of fire throughout each unit. Early growing season burns, for example, reduced the midstory stem density of red maple (a mesophytic hardwood) more effectively but of mesophytic hardwoods overall of 3-6 cm DBH class less effectively than dormant season burns. This pattern may suggest that mesophytic hardwood species other than red maple [e.g. yellow-poplar, blackgum (*Nyssa sylvatica* Marshall), flowering dogwood (*Cornus florida* L.)] responded differently to burn treatments (Phillips and Waldrop 2008), which would have implications for using fire seasonality to manipulate species composition.

Differentiating seasonal fire effects on mesophytic hardwood regeneration is critical if the management objective is to use prescribed fire to reverse the effects of mesophication. A more severe fire could induce equivalent or greater resprouting vigor than a less severe one (Lawes and Clarke 2011), possibly resulting in greater midstory recruitment. Though higher fire temperatures have been shown to maintain or increase red maple sprout abundance (Clark and Schweitzer 2013; Arthur et al. 2015), hotter early growing season burns in our study were still of sufficient severity to reduce midstory red maple stem density more so than dormant season burns. Lower severity dormant season burns, in contrast, may be more effective in reducing the stem density of other mesophytic hardwoods, at least in the short term. It is less clear, however, how the correlation between five severity and sprout abundance persists over time (Brose et al. 2013). Forest midstories with substantial mesophytic hardwood encroachment may see a reduction in the abundance of red maple and mesophytic hardwoods with repeated applications of both dormant and growing season fire (Arthur et al. 2015; Vander Yacht et al. 2019).

Differences in species richness and diversity as a result of season of burn would reflect patterns of recruitment and extirpation, along with shifts in the relative abundance of competing plants. No significant treatment effects for understory species richness or diversity were detected

in this study, a finding which did not support our hypothesis. Changes in the density of understory plant populations that did occur in response to treatments, therefore, were not sufficient to alter community-level patterns of composition. Timing of fire occurrence as it would affect herbaceous vegetation in the early growing season should be considered relative to the physiological breaking of dormancy, even when aboveground biomass is absent (Baskin and Baskin 1988). In contrast to season of burn studies on herbaceous response in the Coastal Plain, growing season burns for this study were restricted to a narrow range of the calendar year (April 18-24) at the very earliest stages of the growing season. Herbaceous plants may not benefit from a favorable growth environment in the early growing season if resource advantages do not compensate for disruption of phenological progression in the spring green-up period. Fire applied during different periods of understory plant growth and dormancy—with effects monitored thereafter—may reveal how season of burn might facilitate shifts in species richness and diversity.

Changes in midstory stem density also may reflect changes in the relative dominance of midstory plants (Baker and Van Lear 1998; Albrecht and McCarthy 2006). The lack of treatment effects for midstory richness and diversity suggest that midstory stems consumed by fire may not have re-recruited into the midstory by the completion of the second growing season following treatment. Reductions in midstory species richness and diversity, observed across treatments, may at least partially reflect the slower recovery of vegetation that has resprouted but not yet reached the midstory. For example, many dead midstory stems of mountain laurel had vigorous basal resprouting accounted for in post-burn measurements of the understory. Though changes in understory sprout density were not significantly different by season of burn (for mountain laurel or otherwise), understory sprouting of many woody species documented in the early growing season may result in changes in species richness and diversity of the advance regeneration layer in later periods post-fire not captured by this study.

Prescribed burns used in this study were unlikely to be of sufficient intensity to cause overstory tree mortality. Accordingly, we did not expect changes in growing season canopy cover as a result of any treatment, or significant differences between treatments. Yet burn treatments reduced canopy cover to a greater extent compared to the unburned control. While such changes in canopy cover were modest, fire may have delayed, second-order effects on the overstory as well. Patterns of litter and duff consumption, as driven by fuel moisture and available fuel, may induce tree mortality as a result of fire spread around the base of the bole (Ferguson et al. 2002). Fire may also cause non-lethal injuries to shrubs and trees, reducing shading in the understory (Yaussy and Waldrop 2010). Changes in understory light availability may alter the moisture environment and thereby levels of surface water retention and fuel moisture (Rodríguez-Calcerrada et al. 2008; North et al. 2005). Therefore, future studies of prescribed fire seasonality should monitor overstory changes after multiple burns and/or over a longer time period.

Management Implications

Early growing season burns had a greater degree and variability of time-integrated heating induced by fire than did dormant season burns, influenced by warmer and drier burn day conditions. Differences in surface fire temperatures by season of burn were most pronounced during the mid-late afternoon on burn days. These patterns of fire behavior correlated with greater probability of fire spread within early growing season burns with fuel moisture being less

of a limiting factor to fire spread. Per given area that fire spread in treatment units, however, surface fuel consumption largely did not differ by season of burn, suggesting that increased levels and duration of heating do not necessarily result in increased fuel consumption. Nevertheless, burning in a given unit in the early growing season is likely to reduce fuel loads at least as effectively as in the dormant season.

Burning during a narrow early growing season window is likely to result in not only higher levels of but also more variable thermal energy release over a greater extent than in the dormant season. This, in turn may result in greater variation in the post-fire vegetation response – possibly enhancing landscape-level community heterogeneity. Topography may limit fire spread and flame lengths in the dormant season more so than in the early growing season. Vegetation response, as influenced by season of burn, has implications for the structure, composition, and function of plant communities. Treatment effects in this study were largely concentrated in the midstory, where growing season burns were most effective in reducing red maple and shrub stem density. Changes in stem density following a single prescribed burn will likely attenuate over time, but prescribed burns applied when seeds have recently been dispersed in the early growing season may be effective for reducing red maple and other mesophytic hardwood abundance.

Managers in the region thus may consider growing season burns as a viable addition to their existing dormant season burning regimes to enhance their ability to achieve their fuel reduction and ecological restoration objectives. They should be mindful, however, of how burning in the early growing season may influence other objectives, including those related to wildlife and smoke.

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Appendix A: Contact Information for Key Project Personnel

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Appendix B: List of Completed or Planned Scientific or Technical Publications and Science Delivery Products

Tours:

5/2018 Southern Blue Ridge Fire Learning Network fieldtrip
6/2018 Clemson University Forest Communities class
9/2018 Clemson University Appalachian Fire Ecology class
6/2019 Clemson University Forest Communities class
10/2019 Clemson University Appalachian Fire Ecology class
9/2020 Clemson University Appalachian Fire Ecology class
10/2020 Clemson University Dendrology class (virtual field tour)
6/2021 Clemson University Forest Communities class (virtual field tour)

Articles in peer-reviewed journals (status in parentheses):

Vaughan MC, Hagan DL, Bridges WC, Dickinson MB and TA Coates (major revisions). How do fire behavior and fuel consumption vary between dormant and early growing season prescribed burns in the southern Appalachian Mountains. *Fire Ecology*

Vaughan MC, Hagan DL, Bridges WC, Barrett K, Norman S, Coates TA and R Klein (to be submitted July 2021). Effects of season of burn on fire-excluded plant communities in the southern Appalachians, USA. Target journal: *Forest Ecology and Management*

Trickett TC and DL Hagan (to be submitted August 2021). Effects of prescribed fire seasonality on the resprout dynamics of southern Appalachian tree species. Target journal: *Fire Ecology*

Melcher A and DL Hagan (to be submitted January 2022). Effects of fire seasonality on forest structure and wildlife habitat in the southern Appalachian Mountains. Target Journal: *Journal of Wildlife Management*

Scientific Conference Presentations and Published Abstracts

Hagan D.L. (2019). Comparing the effects of growing season vs. dormant season burns in the southern Appalachians. North Georgia Prescribed Council Annual Meeting, Jasper, GA. June 2019. INVITED

Norman SP, Vaughan MC, Hargrove WW (2019) Contextualizing Appalachian fire with sentinels of seasonal phenology. In: Proceedings of a conference of the United States-International Association for Landscape Ecology, 2019 April 7-11, Fort Collins, CO.

Hagan D.L. and *Vaughan M.C. (2019). Comparing the effects of growing season vs. dormant season burns in the southern Appalachians. 14th Annual Southern Blue Ridge Fire Learning Network Workshop, Athens, TN, May 14 2019. INVITED

Vaughan M. and Hagan D. (2019). Seasonality of Fire in the Southern Appalachian Mountains. Clemson Biological Sciences Annual Student Symposium, Clemson SC, Apr 6

Vaughan M. and Hagan D. (2019). Seasonality of Fire in the Southern Appalachian Mountains. Natural Resources Graduate Student Association Research Sampler, Clemson SC, Mar 7.

Vaughan M. and Hagan D. (2019). Deriving Meaningful Metrics of Fire Behavior. Appalachian Society of American Foresters Winter Meeting, Wilmington NC, Jan 23-25.

Vaughan, M. Hagan, D. (2018). Deriving Meaningful Metrics of Fire Behavior. Central Appalachians Fire Learning Network Annual Workshop, Blacksburg VA, Oct 23-24.

Technical Workshops for Natural Resource Professionals

Hagan DL (2020). Using seasonality to open the burn window. Consortium of Appalachian Fire Managers and Scientists webinar in the "Fueling Collaboration" series. Dec 17 2020. INVITED

Hagan DL (2018). Forests of the Southern Blue Ridge. Southern Blue Ridge TREX hosted by the Consortium of Appalachian Fire Managers and Scientists and the Nature Conservancy. Oct 29. INVITED

Presentations to Lay Audiences

Hagan DL (2020). Forests of the Southern Blue Ridge. Osher Lifelong Learning Institute (OLLI). Feb 4. INVITED

Hagan DL (2018). Community Meeting: Forest Restoration on the Sumter National Forest. Sept 10, 2019. INVITED

Hagan DL (2019). Forests of the Southern Blue Ridge. Osher Lifelong Learning Institute (OLLI). Feb 4. INVITED

Hagan DL (2018). Forests of the Southern Blue Ridge. Osher Lifelong Learning Institute (OLLI). Feb 22. INVITED

Hagan DL (2017). Forests of the Southern Blue Ridge. Osher Lifelong Learning Institute (OLLI). Feb 1. INVITED

Appendix C: Metadata

The data collected for this project (2016-2020) include fuel (2016-2019), meteorological (2018-2019), topographic, fire behavior (2018-2019), and vegetation data (2016-2017, 2019-2020) as part of a randomized complete block design. Three experimental treatments (unburned control, dormant season burn, growing season burn) were each replicated (blocked) three times. A fourth, standalone dormant season burn treatment in an additional planned replicate was also included for fuel and fire behavior data to equal a total of 10 treatment units. Twenty plots were stratified across a variety of slope, aspect, and landscape positions within each treatment unit (except for 5 plots in the standalone unit). Five plots in burn treatment units were lost due to falling outside constructed control lines, yielding 180 plots as sample units. Each plot was 30 m x 30 m (900 m²), subdivided into nine 10 m x 10 m (100 m²) subplots delineated by 16 grid point intersections and oriented with outer boundaries running magnetic north (0°) and east (90°) from its point of origin. Surface fuel transects (15.24 m in length) were superimposed on each plot, separated by 20° magnetic azimuth emanating from the plot origin. Fuel data include measurements of woody fuelbed height and fine woody debris counts (1-hr, 10-hr, and 100-hr) using a modified version of Brown's Planar Intercept Method (Brown 1974, Stottlemyer 2004), litter and duff depth taken at grid point intersections using 30 cm nails, and surface fuel moisture from grab samples (pooled litter and 1-hr woody, 10-hr woody) on the day of burn prior to ignition. Meteorological data include burn day measurements gathered from the nearest Remote Automatic Weather Station at similar elevation to each treatment unit representing solar radiation, wind velocity, air temperature, fuel temperature, and relative humidity. The Keetch-Byram Drought Index was also gathered for each burn day. Topographic data include Topographic Position Index and Heat Load Index derived from a projected, filled, and clipped digital elevation model and calculated using the ArcGIS Geomorphometry and Gradient Metrics Toolbox. Fire behavior data include time-integrated fire temperatures measured by thermocouple probes and bole char height measured on hardwood tree species at or within 3.05 m of grid point intersections. Thermocouple data loggers were programmed to log temperature at a 1 s interval throughout the burn day, which were then attached to Type K probes, packaged, and buried in the ground approximately 15 cm deep prior to ignition. Probes protruded aboveground and were oriented such that the tip faced downward at a uniform height of 2.54-5.08 cm above the litter surface. Vegetation data include understory, midstory, and overstory cover, density, and/or height identified to the species level when possible and grouped according to growth habit, tree group, and management species of interest when applicable. Understory plants were sampled within 1 m² quadrats based on a modified form of the Carolina Vegetation Survey (Peet et al. 1998), with individual woody plants tallied at or above the root collar within life history and height classes. Midstory and overstory plants were sampled within 5 of 9 subplots per plot with midstory stems grouped by diameter class and overstory stem diameter measured at breast height. All files are in .xlsx format and contain a metadata worksheet that describes each field. The data and accompanying metadata will be archived in the Forest Service Research Data Archive upon publication of journal articles presenting the data. Files include the following:

Fuel (fine woody debris) – 2016, 2017, 2018, 2019 Fuel (litter and duff) – 2018, 2019 Fuel moisture – 2018, 2019 Meteorological (RAWS/WIMS) – 2018, 2019 Topographic (TPI, HLI) Fire behavior (thermocouple) – 2018, 2019 Fire behavior (bole char height) – 2018, 2019 Vegetation (understory) – 2016, 2017, 2019, 2020 Vegetation (overstory) – 2016, 2017, 2019, 2020 Vegetation (overstory) – 2016, 2017, 2019, 2020